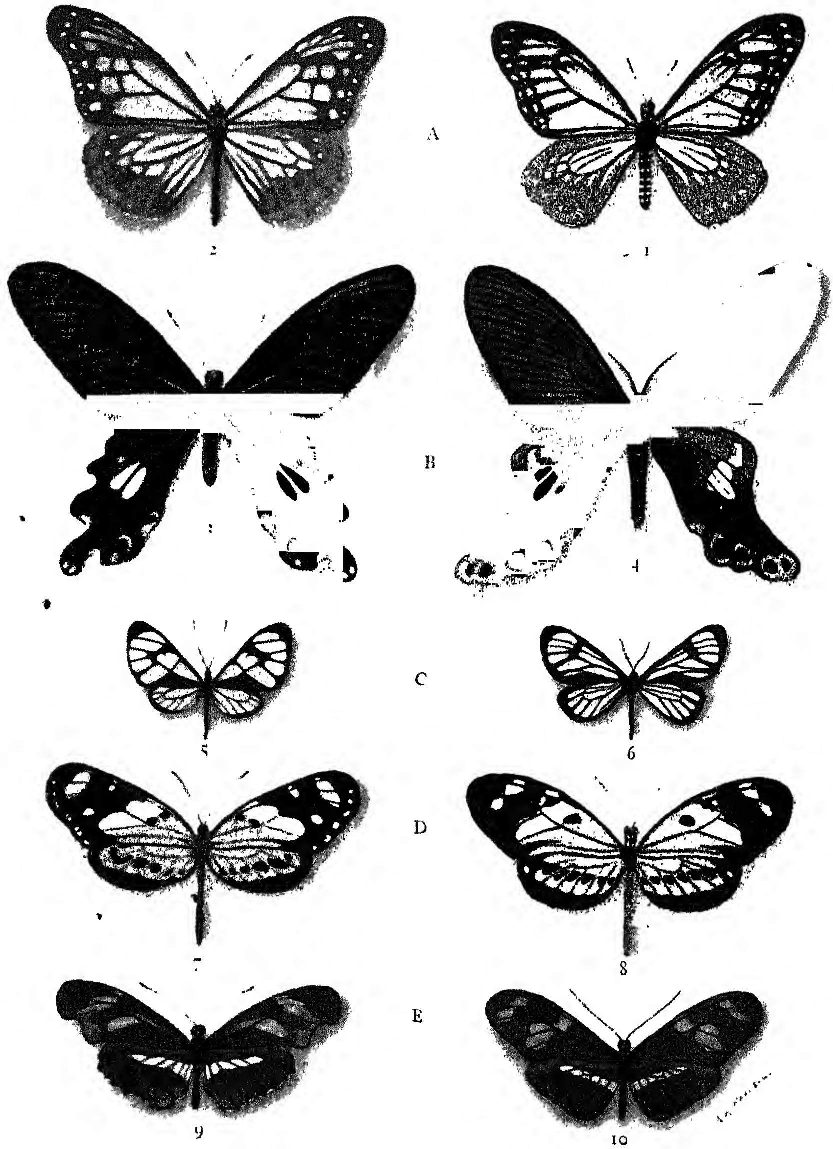
PLATE I.




"MIMICRY" IN BUTTERFLIES

1—*Papilio agestor* ; 2—*Caduga* (or *Danais*) *tytia* ; 3—*Papilio bootes* ; 4—*Epicopeia polydora* ; 5—*Ithomia diasia* ; 6—*Gerra hyelessides* ; 7—*Melinaea paraiya* ; 8—*Heliconius robigus* ; 9—*Colaenis telesiphe* ; 10—*Heliconius telesiphe*.

# EVOLUTION

BY

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# PREFACE

This is a book for beginners. Its object is to provide a sketch in outline, approximately correct in its proportions and not overburdened with detail, of the evolutionary science of to-day.

I am one of those who believe that a grasp of the main principles of biological science, and amongst these principles Evolution is one of the first, is an essential part of the intellectual equipment of the citizen of the modern state; and I look forward to the time when a course in elementary biological science—not details of anatomy and physiology, but broad general principles—will form an integral part of the normal curriculum of our schools.

My sketch of evolution is a frankly personal one. Having learned my lessons in the open and in the tropics, as well as in the laboratory, I have not hesitated to accord to field natural history what I regard as its rightful place in relation to evolutionary theory. Nor, while compelled by my experience to be a follower of Charles Darwin, have I hesitated to adopt various modifications in detail in my presentment of the subject. For example, the potency of Natural Selection in

encouraging variability along definite lines, and the importance of change of environment as a factor in evolution, are as I believe by no means generally appreciated, and are therefore emphasized in this book.

Among the friends who have helped me in various ways I ought to make special acknowledgement to two—Mr. James Chumley, who has been kind enough to read and re-read the volume in proof, and Mr. A. K. Maxwell, whose exquisite skill as an artist is responsible for the originals of the two coloured plates. The beautiful photograph of fishes on p. 154 I owe to the kindness of Professor W. H. Longley.

J. GRAHAM KERR.

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## IN TEXT

"It occurred to me that something might perhaps be made out on this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it."—CHARLES DARWIN, *Introduction to the Origin of Species.*

"The characteristic of erroneous theories is that they can never produce new facts, and every time that a fact of this kind is discovered, these theories are obliged, in order to account for it, to graft a new hypothesis on to the old one."—LOUIS PASTEUR.

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"We stand, in these times, upon a calm elevation of intellectual attainment, and not in the dark recess of mental deprivation. Proof is what I require—proof, and not assertions. . . . 'Mr. Snobee,' said Mr. Wilson, 'is a fit and proper person to represent the borough in Parliament.' 'Prove it,' says I. 'He is a friend to Reform,' says Mr. Wilson. 'Prove it,' says I. 'The abolitionist of the national debt, the unflinching opponent of pensions, the uncompromising advocate of the negro, the reducer of sinecures and the duration of Parliaments; the extender of nothing but the suffrages of the people,' says Mr. Wilson. 'Prove it,' says I. 'His acts prove it,' says he. 'Prove *them*,' says I.

"'And he could not prove them,' said the red-faced man, looking round triumphantly."—CHARLES DICKENS (*Sketches by Boz*, Characters, Chapter V. "The Parlour Orator").

# CHAPTER I

## INTRODUCTORY

Perhaps the most startling intellectual difference between the last half-century and its predecessors lies in the extent to which all departments of human thought have come to be permeated, and indeed in many cases dominated, by the idea of Evolution. In the sayings and writings of philosophers, politicians, theologians, historians, in fact throughout the literature of the day, we find the word evolution constantly cropping up. In the domain of physical science, where only a few decades ago we were taught to think of the chemical elements as substances fundamentally distinct in their nature, we find the teaching of to-day emphasizing the probability that the so-called elements are merely successive stages of change of one primordial substance. What used to be regarded as quite distinct and independent types of energy—electricity, heat, light—we find now strung together as manifestations of movement in a continuous gamut of varying wave-length. Even the supposedly fundamental difference between matter and energy is disappearing, and we are taught that the ultimate units out of which matter is built up are in themselves not matter at all, but merely charges of a particular kind of energy—the whole of the phenomena of the

dead universe around us being thus reduced to varied manifestations of one ultimate existence.

But it is with the living world—of plants and animals and protists—that the idea of evolution is most strongly associated. No doubt in itself the general idea of evolution is a very old one, dating back to a period far anterior to those classical writings from which references to it are often quoted, back to the days when primitive man, long before the beginnings of literature, began to wonder vaguely whether the world around him, with its plants and beasts that meant so much in his ordinary life, had not come into being by a process of gradual growth or evolution. But the actual demonstration of the truth of the evolution theory, so that its acceptance was forced upon every one, was the work of a modern biological philosopher, and the materials he made use of were facts regarding living organisms.

The ultimate object aimed at in the work of the human intellect, whether it be called Science or Philosophy, is to determine the general principles or laws which link together the phenomena of Nature. As investigation proceeds larger and larger numbers of facts are found to fit together into natural groups or series, until it may be some relatively enormous mass of facts is found to fit into a continuous series definable by one general expression or formula. Such general expressions are exemplified on a grand scale by the words Gravitation and Evolution. The progress of Science or Philosophy consists of the seriation of larger and larger bodies of facts under one expression,

but it begins with the simple linking of one fact to another. The humble worker who establishes that two facts are really connected which appeared to be isolated is thereby making a definite contribution to scientific advance. A primitive tribe of savages amongst whom I once lived distinguished the three species of palms which grew in their territory by three quite distinct names. They appreciated the differences between the three species, but they failed in the higher mental effort expressed by the group word palm which links them together into a series. This simple example brings out clearly what is one of the fundamental principles of intellectual advance. Its importance has to be borne in mind more particularly in a period of unrest like the present when the disappointed investigator too commonly develops the symptoms, either of despair or of the intellectual topsyturvydom betokened by his devoting his main energies to the comparatively easy task of laying bare previously undetected *differences*, ignoring the fact that thereby he is abandoning one of the first principles of scientific progress.

Were an adult human being with his complete observing and thinking equipment to be suddenly dropped down into this world of ours, undoubtedly one of his first impressions would be that of the apparently endless variety of the phenomena and objects he sees around him. In a very short time, however, he would begin to appreciate the fact that these phenomena and objects are not all absolutely different: he would recognize distinct kinds, or groups, of the same type. Were he

looking specially at the animals or plants, for example, he would very soon learn to recognize groups of individuals united to one another by definite likenesses and marked off from others by definite unlikenesses: he would recognize in fact different kinds or *species* of animals or plants—but each of these would seem different from all others. As his education proceeded he would begin to appreciate the fact that no more are the different species absolutely different than are the different individuals. Just as the individuals are linked together into species, so in turn he would perceive that the different species are also linked together by likeness into groups of a higher order. The attainment of this conception of *generic* ideas is a long step beyond the recognition of species, and this step is followed by further similar steps by which groups of higher and higher order are recognised: families, orders, classes, phyla, and so on.

When things seem entirely different it is natural to regard them as always having been so: if any speculation is entered into as to their origin it is natural simply to conclude that they were created different in the beginning. But once it is recognized that they show these differing degrees of resemblance to one another it is a natural enough idea to wonder whether the resemblance is not really a kind of family likeness, due to closer or less close blood-relationship. According to the theory of evolution this is actually the case—all the differences that are so conspicuous in the universe to-day have developed out of a primitive condition in which the whole universe was alike and homogeneous.

While this general idea is a very old one, its

working out in detail and its elevation to the position of a scientific theory are achievements of the last century. They followed the work of the great cataloguers of living things—the systematists who laid bare the natural classification of animals and plants. The foundation stone of this classification is the conception of species or kind—in itself one of the very oldest conceptions in regard to living things, dating back indeed to pre-human stages of evolution. The conception of species was given a more precise form by John Ray (1628-1705), a student and teacher of classics and theology at Cambridge, who classified plants and animals into species and groups of species according to their anatomical structure. Ray's work paved the way for that of Linnaeus (1707–1778), the greatest of all systematists. Linnaeus in his *Systema Naturae* (1735) aimed at a descriptive catalogue of the mineral, vegetable, and animal kingdoms so far as known in his time. He introduced crisp, concise, exact descriptive terms, and he used the classificatory groups which we still use—varieties, species, genera, orders, classes, and thus brought order out of chaos. Each species was furnished with a Latin name and a short descriptive diagnosis, and when referred to was quoted according to the binominal system, *i.e.* by giving the name of the genus, followed by that of the species. The Linnaean *Systema Naturae* still forms the basis of the modern classification of plants and animals, and in any systematic work on animals or plants one may still see species names followed by the letter "L." or the contraction "Linn.", indicating that the name of the particular species has come down to us from Linnaeus.

To Linnaeus as to the biologists of to-day the "species" was the main unit of classification. The word species corresponds to the ordinary word "kind", and in German the words species and kind (*Art*) are still interchangeable, and this is of advantage, for it helps to guard against the conception of species assuming in one's mind too rigid and precise a character. The title of Darwin's great book, *On the Origin of Species*, is apt to induce this: so also are the studies of specialists who, developing in their minds a fairly precise idea of what is a species within their own special group, are apt to extend their conception beyond its boundaries. As a matter of fact, there is no correlation between the amplitude of the conception "species" as used in one group and as used in another. A classifier of dipterous flies, or of oligochaete worms, or of mammals, or of corals, becomes able to formulate in his mind a more or less precise idea of what he means by "species", but this idea is of little value outside the boundaries of his group. It is one of the very few evil effects of the publication of the *Origin* that it has tended, by its title, to foster the idea of "species" being equivalent throughout the realm of living nature. The same argument applies to other group names —variety, family, order, class; any one of these connotes a more or less definite idea within the limits of a single group of higher order, but only within these limits. There is a real danger—encouraged by specialists in taxonomy—of the student getting into his head the idea that the scheme used by the zoologists of the day in classifying animals is a rigid framework existing in nature into which every animal must be made to fit exactly,

instead of being as it is merely a convenient way of expressing contemporary knowledge.

For Linnaeus species were still absolutely discrete: each species consisted of the descendants of one pair of original ancestors independently created: and the spirit of Linnaeus still lingers on in the work of many systematists who in forming new species are naturally apt to be more interested in the differences rather than in the resemblances between organisms. Already, however, as the eighteenth century went on the idea of evolution began to obtrude itself. Goethe—poet and naturalist—perceived that the petals and stamens of a flower were fundamentally equivalent to leaves. Erasmus Darwin, Lamarck, and others formulated definite evolutionary theories, but it was left to Charles Darwin to give the convincing demonstration of the fact of evolution, and in providing this demonstration Darwin made what is perhaps the greatest contribution that has ever been made to the sum of human knowledge. There is probably no department of human knowledge that has not felt its vitalizing influence.

I propose in this book not to do anything in the way of tracing out the historical development of the evolutionary idea, though that is a fascinating story, but simply to sketch in outline the theory of evolution as it presents itself to my mind to-day. Further, I propose to restrict myself to the animal kingdom, ignoring plants and ignoring protists, in the first place because I am personally less ignorant regarding the animal kingdom, and in the second place because I believe much liability to

error is introduced into evolutionary speculation by the absence of such restriction. The animal and the plant kingdoms diverged from one another at a very remote evolutionary period, and I believe that some of their most striking resemblances, such, for example, as the phenomena of mitosis and of fertilization, have been developed by them quite independently. Unless we take care to keep the data regarding the two kingdoms rigidly apart we are very liable to be led into error, in the way of false interpretations and even of false observation. On the other hand, if we keep the two sets of data apart and build up our theory of evolution independently for the two kingdoms, it becomes then of fascinating interest to note the parallelisms and divergences of evolution in the two kingdoms; how in order to do corresponding work mechanisms are evolved in some cases extraordinarily similar, such as mitosis, the mechanism of nuclear division, in other cases extraordinarily different, such as that of nutrition.

As our knowledge of living things has gradually advanced there has come about a tendency for that knowledge to become subdivided into two main sections—the one including facts and theories in regard to structure (morphology), and the other facts and theories in regard to function (physiology). This subdivision is obviously natural, inasmuch as it expresses the tendency, indeed the necessity, of investigators in order to be successful, to become specialists in one or other of the different types of technique required for the investigation of the two types of phenomena. But it must ever be borne in mind that in the living animal structure and function are inseparable. A book on evolution

must be to a preponderating extent morphological, for the simple reason that the *record* of evolution is entirely morphological. The evolution of structure is as we shall see duly recorded in symbols consisting of structural details, the corresponding evolution of function leaves, as a rule, no such natural record behind it. It is necessary to emphasize this consideration, for failure to appreciate it is constantly making itself conspicuous in evolutionary discussions, as, for example, when it is said that some higher development of function was made possible by the higher development of a particular organ, or when a blank in some paragraph of evolutionary history is filled up by assuming the existence of an intermediate type of structure which by no possibility could be efficiently functional.

Another consideration that deserves emphasis, because so often forgotten, is that Evolution is a philosophy of wild nature. It relates to animals living under natural conditions, outside the domain of the laboratory worker and in that of the field naturalist. The laboratory-trained zoologist lacking in field knowledge often shows a singular incapacity for understanding the importance of evolutionary factors which experience in the field, more especially tropical experience, drives home—such as, for example, the intensity of the struggle for existence or the adaptive significance of animal coloration.

Again must one guard against the intrusion into speculations regarding secular evolution of considerations of time as measured by human units. Such expressions as centuries, or thousands or millions of years, have no meaning in relation to evolution. To the periods of time in which secular

evolution has taken place the entire period of human history is but an instant, and the failure to perceive evolutionary change taking place before our eyes means as little as it does to gaze out at night upon a stormy sea and observe by the light of a single lightning flash that all the waves are still.

Finally, I would have it borne in mind how little relatively we know about living things and living processes. The teacher of zoology when he begins to teach about the simplest creature in his course—*Amoeba*—finds himself held up by almost complete ignorance regarding some of the most fundamental points in its physiology. Our knowledge is, and always must be, comparatively superficial as compared, say, with the physicist's knowledge of physical phenomena, for the reason that we cannot apply to living substance the method of analysis—the method of splitting the complex into its simple components, and the investigation of these in the isolated condition—the method which has yielded to physics and chemistry their triumphs. What we have to do in biology is to observe the exceedingly complex phenomena with which we are concerned to the highest degree of accuracy attainable by the most highly developed technical methods, and then to endeavour to seriate our observations, so that they divulge general principles or so-called "Laws". And we should not forget that these are, up to the time when they can be finally accepted as demonstrably true theories, mere "working hypotheses" which appear to bring into logical relation to one another a particular array of facts. Such a hypothesis is to be accepted and retained so long as it accomplishes this function

more satisfactorily than any other available hypothesis, but is to be abandoned at once if a more efficient substitute presents itself. On the other hand, it should be remembered that a working hypothesis during the early stages of its development into a true theory is necessarily imperfect, and no particular heed need be paid to the armchair critic who points out that "this theory does not explain" so-and-so, or "on this theory it is difficult to understand" so-and-so.

## BOOK FOR FURTHER STUDY

Osborn. *From the Greeks to Darwin.*

# CHAPTER II

## EMBRYOLOGY

THE science of Embryology deals with the process of development by which the fertilized egg or *zygote* gradually takes on the form of the adult animal.

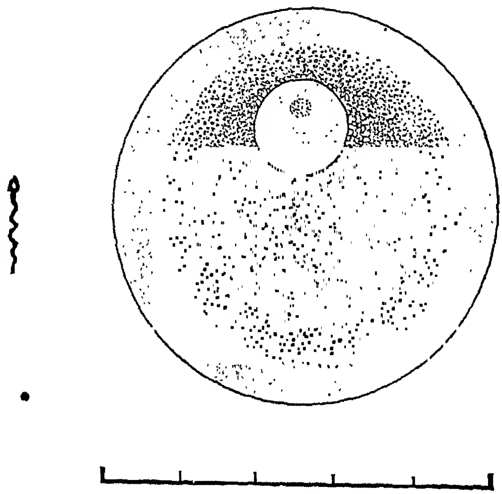


FIG. 1.—Human gametes highly magnified: egg to the right, spermatozoon to the left. (From Bower, Graham Kerr, and Agar, *Lectures on Sex and Heredity*.) Each division of the scale represents ·05 mm., or about $\frac{1}{500}$ inch.

Its special interest to the evolutionist lies in the fact that when we study the developing individual of any species of animal we see the process of evolution going on before our own eyes. If we are

studying one of the more complex types of animal we find that it normally begins its existence in the form of a single cell, the zygote, which has come into existence by the fusion or *syngamy* of two reproductive cells or *gametes* (cf. Fig. 1) derived one from each parent. Now if the zygote advanced no further in development, if it simply went on leading its life as a unicellular creature, we should include it in the group of animals known as the Protozoa: the zygote is in fact a transient protozoan phase in development.

As a matter of fact, however, the zygote does not retain its unicellular condition: it undergoes fission or division into two cells; each of these repeats this process of fission, and the process is repeated over and over again, the original zygote being represented by an ever-increasing number of cells, all descendants from it and all adherent together and constituting the multicellular body of the individual. In a large number of cases, belonging to the most varied groups of animals, an early stage is passed through called the *gastrula*—a more or less cup-shaped organism with a double wall composed of two layers of cells (ectoderm and endoderm) enclosing a cavity open to the exterior by a primitive mouth opening (Fig. 2). Now if the animal remained in this stage of development, retaining its two-layered wall and its simple mouth, throughout its life, no zoologist would have any difficulty in classifying it. He would recognize it as a simple member of the great group of primitive animals called the Coelenterata. The gastrula in fact is a temporary coelenterate stage of existence.

Or suppose we are studying the course of development of one of the most complex types of

vertebrate animal—say a bird or a man—we find that there gradually emerge the characteristics that enable us to identify it as belonging to the group Vertebrata, but for a time its organization is that of a far more lowly type of vertebrate than the adult. In its skeleton we find no complicated backbone, but only the simple elastic rod or notochord that we find, in adult life, only in some of the most lowly types of fish. At the sides of its neck we find a number of slit-like gill-openings corresponding

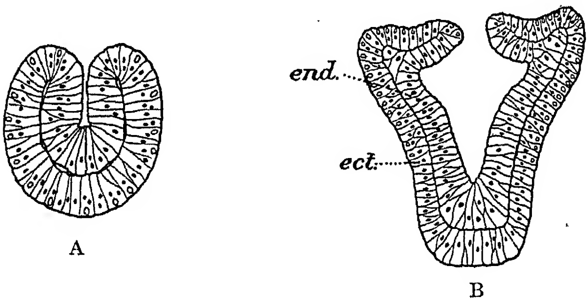



Fig. 2.—Early stages in the development of the common jellyfish (*Aurelia*) as seen in longitudinal section under the microscope. (From Graham Kerr, *Zoology for Medical Students*.) A, gastrula stage; B, young hydroid stage; *ect.*, ectoderm; *end.*, endoderm.

to those which the water-inhabiting fish uses for breathing. In the bird or the man they will of course never be used, but there they are, present in the young embryo. If we examine the main arteries we find these are arranged as a series of aortic arches passing up between successive gill-clefts. In the fish these convey the blood to the gill-clefts—there to be oxygenated: in the bird or the man there is no functional reason for the blood being carried in this way to the gill-clefts, but nevertheless it is so carried—precisely as in a

fish. If we examine the heart we find it in the form not of the complex organ with its various chambers and valvular openings that we know in the adult man or bird, but in the form of a simple tube with waves of contraction running along it, just as we find in the case of the lowest type of heart. Finally, if we look at the limbs we find not the complicated and highly specialized legs and arms or wings of the adult—but crude, simple, flipper-like structures.

Now if a naturalist found a creature retaining in its adult state these various characteristics he would have no difficulty in allotting it to its main subdivision of the Vertebrata: he would at once class it as a fish: it is in fact a fish stage of development.

We are then justified in asserting (1) that the individual in the case of the more complex animals goes through a regular process of evolution during its life-history, and (2) that occasional stages in this evolution are recognizable as presenting types of structure characteristic of the adults of less highly organized groups.

As to the significance of this extraordinary fact we have only one explanation open to us—namely, that it is due, like the other characteristic features of the particular creature, to the workings of heredity. We possess five fingers or any other of our natural characteristics because we inherited them from our parents and more remote ancestors. Similarly we possess for a time fish-like conditions of various organs because we inherit them from ancestors. But we must go further. If the fish-like condition of an organ was present in our ancestors it must have been actually functional.

If gill-clefts with their rich supply of blood were present in these ancestors they were there for use—for breathing water. In short, the occurrence of a fish stage during the individual evolution of a bird or man necessarily implies a fish stage in the past history of their race.

If instead of regarding the individual as a whole we confine our attention to its constituent organs we again see the same process taking place, the organ going through a definite process of evolution. If, for example, we study the skeleton of a man at the various periods of his development we find that it exists first as a mere notochord—as is still to be seen existing in the adult of the very lowest type of fish, later on as a purely cartilaginous skeleton, such as is again found in the adults of comparatively lowly organized fish, and it is only in its final stage that it assumes the bony condition characteristic of the adults of the more typical vertebrates. If again we study the development of the great arteries of the human being we find that, as already indicated, they pass through the condition characteristic of a fish, there being a series of aortic arches arranged for the re-oxygenation of the blood in the gills—although in man these gills will never be used. Or again, if we study the development of the liver we find that at first, instead of being the exceedingly complicated organ seen in the adult, it is in the form of a simple pocket-like extension of the wall of the intestine, as we see it in the adult *Amphioxus*—the lowliest of all vertebrates.

The study of embryology then displays to us the process of evolution taking place during the development of the individual animal and so, in

view of the fact that the characteristics of each type of animal are inherited from its ancestors, provides us with convincing evidence that living creatures as we see them in the world to-day are the product of a process of racial evolution. Not only so, but the fact that the individual during his development passes through stages representing stages in the development of the race indicates to us that we may justifiably expect embryology to provide us with many clues as to otherwise unknown details of racial evolution.

A natural result of the widely spread recognition of this principle of embryonic recapitulation during the years immediately succeeding the publication of the *Origin of Species* was that numbers of enthusiastic workers in the various schools of zoology devoted themselves to investigating the embryology of different types of animals, in the belief that thereby they would obtain a complete and accurate picture of their past evolutionary history. These early enthusiasts failed, however, to realize as we do now that the matter is not so simple as it at first seemed, and that disturbing factors are at work which render the embryological picture of racial evolution incomplete and in many cases very deceptive.

We have to realize in the first place that every living creature has its whole organization intimately adapted to its own particular mode of life: this applies not merely to the adult but to every phase in its development. Now the mode of life of early developmental stages is commonly very different from that of adult animals. We have seen, for example, that one of the higher vertebrates, such as a man or a bird, passes through a fish stage in

its development; but the mode of life of this stage, living in the one case as a parasite within the body of its mother and feeding by processes of diffusion between its blood and hers, and in the other case as a prisoner cooped up within an egg-shell and subsisting on the stored-up food material or yolk, is clearly very different from that of a free-living fish. Consequently we should have every expectation that features directly related to the free mode of life of an ordinary fish would completely disappear in the fish stage of individual development and be replaced by new adaptive features fitting it for its embryonic mode of life. This we find is actually the case, and this tendency for ancient ancestral characters to be replaced by new adaptive ones constitutes one of the main disturbing factors that interfere with the perfection of the record of evolution provided by embryology. It consequently becomes one of the great tasks of the embryologist to decide in any given case whether a particular feature is ancient and ancestral, or modern and adaptive.

This is not the only factor that interferes with the embryological record of evolution. In a completely developed animal which lives its own life and works for its own livelihood the various organs of the body are necessarily at corresponding stages of development, so that they can all work together as parts of the organic whole. In the embryo, developing within the egg-shell or uterus, on the other hand, there is not the same need for the various organs to be at a corresponding stage of development: they need not keep, so to speak, exact pace with one another. The result is a tendency to fall out of step, some organs tend to

hurry on with their development—others to lag behind. In particular there is a tendency for organs of great complexity of minute structure—such as, for example, the brain or the eye of a vertebrate—to reach a large size during comparatively early stages of development so as to allow, as it were, plenty of time for the elaboration of the complicated minute detail.

It might be suggested that such disturbances of the evolutionary record would not occur in those animals which go through what is termed a larval type of development, *i.e.* where the young stages live their own independent life just as much as does the adult. Such a suggestion, however, would be fully acceptable only in cases where the young animal still retains unchanged the mode of life characteristic of the ancestor. In a few cases we are justified in believing this to be the case. For example, in the three ancient groups of vertebrates represented by *Polypterus* (Crossopterygii), *Lepidosiren* (Dipnoi), and the tailed Amphibians, we find larvae (Fig. 3) showing deep-seated similarity in structure which we are probably justified in accepting as repeating, with only comparatively slight modification in detail, the form of the common ancestor, which in all probability lived very much the same kind of life as do these larvae to-day.

On the other hand, many types of larvae have probably no close resemblance to ancestral stages of evolution. Such is, for example, the well-known *Nauplius* larva (Fig. 4, A) occurring in the life-history of many of the Crustacea. It is found to be a general characteristic of the individual development of segmented animals with elongated bodies and a definite head end, that development takes place

from the head end backwards, the various segments of the body, except the terminal one, appearing in regular sequence one after the other. Such accelerated development of the front part of the body as compared with the hinder part reaches its maximum in the nauplius larva, which is simply the precociously developed head with its three

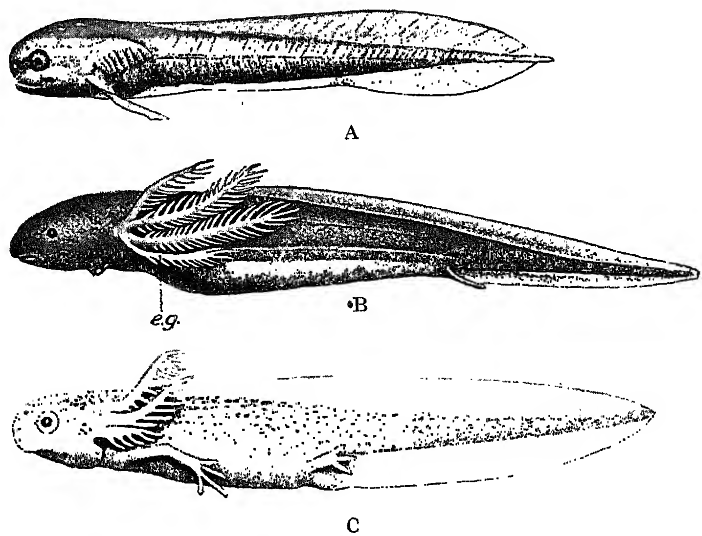



FIG. 3.—Larva of (A) *Polypterus*, (B) *Lepidosiren*, (C) a newt (*Triton*). (A and B, from Graham Kerr, *Embryology*; C, after Glaesner.) *e.g.*, external gill.

first pairs of appendages. It is exceedingly improbable that the common ancestor of those Crustacea possessing this type of larva had any close resemblance to the nauplius. It is more reasonably to be regarded as an exaggeration of the tendency already alluded to for the headward parts of the body to precede the tailward in development. At the same time the nauplius larva is of great importance in relation to the evolutionary

study of the Crustacea, for the tendency to develop this particular type of larva is clearly a valuable sign of blood-relationship. Thus its presence in the life-history of certain Cirripedia (barnacles) betrays the fact that these highly specialized creatures are Crustacea which have become so

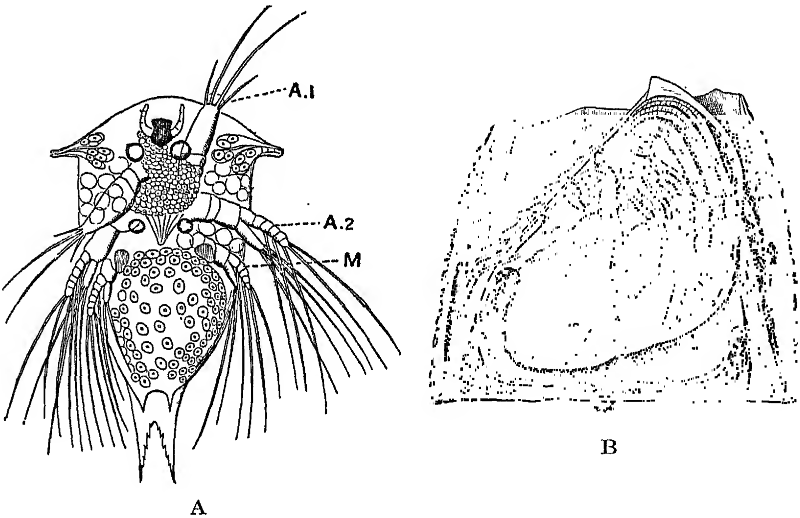
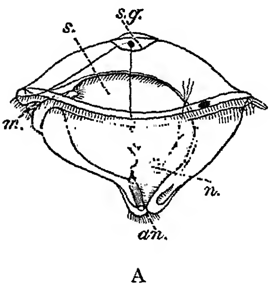


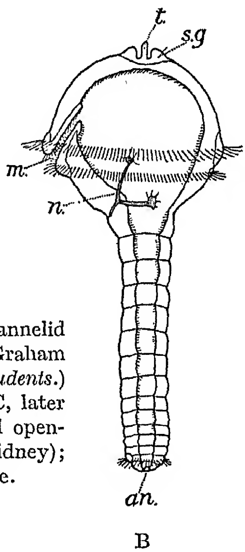

FIG. 4.—A, a "Nauplius" larva; B, an adult rock-barnacle (*Balanus*). (A, from Geoffrey Smith, *The Cambridge Natural History*; B, after Darwin.) $A_1$ and $A_2$, antennae; M, mandibles.

modified as to be otherwise hardly recognizable as such (Fig. 4, B).

A case very similar is that of the *trochosphere* larva, characteristic of many kinds of marine worms and molluscs. The trochosphere (Fig. 5, A) is rounded in form and is propelled through the water by the beating of numerous cilia arranged in a belt round its equator. The mouth (*m.*) is situated at one side in the neighbourhood of this belt, while the anal opening (*an.*), by which useless

waste matter is got rid of, is situated at the posterior pole. At the opposite pole, which goes in front when the larva swims, is a primitive brain (*s.g.*) and simple sense organs. A glance at Fig. 5 shows



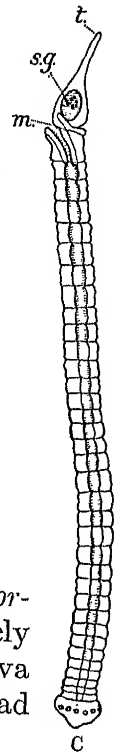




FIG. 5.—Life-history of a simple annelid worm (*Polygordius*). (From Graham Kerr's *Zoology for Medical Students.*) A, trochosphere larva; B and C, later stages in development. *an.*, anal opening; *m*, mouth; *n*, nephridium (kidney); *s*, stomach; *s.g.*, brain; *t*, tentacle.

how the worm therein represented (*Polygordius*) has in its early stages (B) an immensely swollen head, and that the trochosphere larva (A) is simply this precociously enlarged head which has not yet grown a body.

The nauplius and trochosphere by no means exhaust the types of pelagic larvae. By towing a fine gauze-net slowly in a calm sea and examining the catch with a microscope it can be seen that the surface waters are populated by a wonderful variety of larvae (cf. Fig. 6) of bizarre and often beautiful form. These glide hither and thither through the water, propelled by their cilia, their most conspicuous differences from the trochosphere

being that, to gain increased power, the ciliated band has increased greatly in length, meandering in curves over the surface of the body (A), or in some cases extending out on to slender projections which have grown out from the body to provide

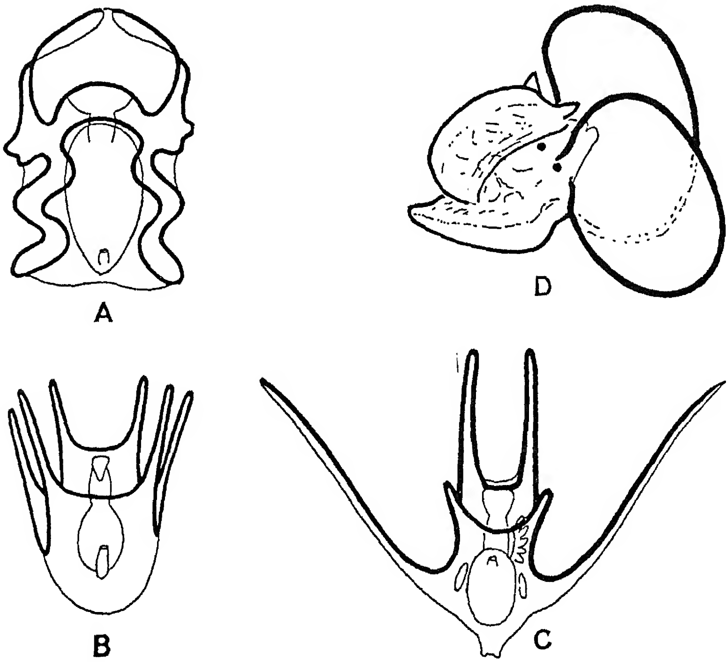



FIG. 6.—Larvae of various marine animals. A, a Holothurian (*Auricularia*); B, a sea-urchin (*Echinopluteus*); C, a brittle-star (*Ophiopluteus*); D, a Gasteropod (*Veliger*). The band of cilia is shown by the thick black line. In A it meanders over the surface of the body; in B and C it extends out along slender projections; in D it circles round the edge of two thin flat flaps.

greater accommodation for the lengthening band (B, C, D).

We are probably not justified in regarding any one of these pelagic larvae as representing closely a stage in ancestral evolutionary history. Each

one has developed its main characteristics as adaptations to its peculiar pelagic mode of life. But yet each one is of interest and of potential importance to the student of evolutionary zoology, for any one of them may on occasion solve a difficulty as to the blood-relationship of some new type of animal. For example, were we to find some new animal whose adult structure failed to yield distinct clues as to its affinities, and then to discover that it had a larval stage of the Ophiopluteus type (Fig. 6, C), that fact would constitute strong evidence that the affinities of the animal were with the group of star-fishes known as Brittle-stars (Ophiuroidea).

I have tried to give an indication of the kind of distortions which affect the embryonic recapitulation of evolutionary history, but we must not allow the existence of such distortions to blind us to the main fact of recapitulation—the fact that the individual, or the organ of the individual, goes through a process of evolution during the early stages of its life-history, and that the stages of this process frequently give us information regarding stages of the racial evolution through which the ancestors of the particular animals have passed.

# CHAPTER III

## PALAEONTOLOGY

We have seen in the preceding chapter that the facts of ontogeny—the embryological development of the individual—leave us no option but to accept as a fact the process of secular racial evolution during the past.

But if we are correct in our acceptance of racial evolution as a fact it is clear that we should expect to find some record of it in that history of past geological eras which is constituted by the rocks with their petrified remains of long extinct animals.

Geologists have been able to work out the chronological sequence of the main fossiliferous rocks which form this geological record, and have given names to the successive chapters or formations as shown in the accompanying table:

TABLE OF GEOLOGICAL FORMATIONS

| | |
|---|---|
| Quaternary | Present day and Recent.<br>Pleistocene. |
| Tertiary | Pliocene.<br>Miocene.<br>Oligocene.<br>Eocene. |
| Secondary or Mesozoic | Cretaceous.<br>Jurassic.<br>Triassic. |
| Palaeozoic | Permian.<br>Carboniferous.<br>Devonian and Old Red Sandstone.<br>Silurian.<br>Ordovician.<br>Cambrian. |
| | Precambrian |

Before as evolutionists we proceed to consult this geological history it is necessary to have some idea as to how much we are justified in expecting from it.

Naturally we should ask as a preliminary: Do these rocky deposits provide us with a continuous record from the commencement to the end of the period of time which they represent? Quite the contrary!

In the first place, the rocks which yield fossils form only a very small percentage of the whole series of sedimentary rocks.

In the second place, the various chapters of the Geological Record, the various formations as the geologists call them, are not continuous with one another but are spaced out by intervening gaps representing vast, although quite indeterminate, periods of geological time.

Next we have to bear in mind that the only portions of animals which are normally preserved as fossils are hard skeletal structures, such as bones and shells. But skeletal formation itself marks an advanced stage in evolution. Many types of existing animals of the greatest importance from the evolutionary point of view have either no skeleton, or no skeleton of a preservable nature, and the same was undoubtedly the case with multitudes of archaic types of animals in the past, whose evidence would be of the greatest use to the evolutionist, but which, owing to their not having developed a skeleton, must for ever remain unknown.

Again it is clear that even in the case of animals possessing a skeleton suitable for fossilization it is only comparatively rarely that an individual is

entombed in such a way as to ensure its persisting as a fossil. In the immense majority of cases the whole body including the skeleton simply disintegrates after death into unrecognizable particles.

When we bear in mind such considerations we realize how ridiculously imperfect must be the record of evolution embodied in the rocks.

Imperfect as is the geological record, how infinitely more imperfect must necessarily be our knowledge of that record! The largest mines, quarries, and other excavations made by man, are in themselves relatively insignificant scratches on the surface of the vast mass of fossil-bearing rocks, but yet how small a fraction of the material obtained in such excavations ever passes under the detailed scrutiny of the palaeontologist.

A full appreciation of the importance of these factors affecting the geological record will lead the inquirer to approach that record not with the expectation of finding in it a complete history of evolution but rather with the doubt whether it is worth while to consult it at all; and the further doubt whether any evidence that might be afforded by it would not be so scrappy and incomplete as to be hopelessly misleading and unreliable. As a matter of fact, however, any one approaching the geological record in the properly chastened frame of mind induced by the considerations I have indicated cannot fail to be astonished and delighted by the beautiful and incontrovertible bits of evolutionary record which it has already revealed. The most striking of these are occasional little paragraphs of evolutionary history which good fortune has placed in the way of the palaeontologist and enabled him to decipher in detail. As an example of such

paragraphs I will summarize one of the best known, that relating to the evolutionary history of the horse as worked out by the palaeontologists of North America.

### The Evolution of the Horse

The modern horse is one of the most peculiar and highly specialized of mammals: its specialization fits it for rapid movement over dry plains and for subsistence on harsh grassy vegetation. This specialization shows itself particularly in the structure of its limbs and teeth.

The limbs are of great length. Their joints are of such a nature as to allow only a simple backward and forward swinging movement, and the great masses of muscle are concentrated at the upper end of the limb so as to cause the centre of gravity to be very high. The shortening of the natural period of the pendulum-like swing due to this raising of the centre of gravity is obviously of the greatest importance in facilitating rapidity of movement. The foot is greatly simplified: it has only a single toe or digit, and only the tip of this, ensheathed in the exaggerated and modified claw that we call the hoof, touches the ground.

Fig. 7 (B) shows the details of the skeleton of the hind-foot of the horse as compared with that of *Phenacodus* (Fig. 7, A), a more ancient type of mammal which shows much less striking differences from the normal mammalian type. In *Phenacodus* we see the set of bones characteristic of an ordinary mammal. At the upper end are the small compact bones of the ankle, or tarsus, arranged in an upper (proximal) and a lower (distal) row with a single

bone (navicular) between. In the proximal row are two bones, the astragalus, which bears the actual joint surface, and the calcaneum or heel-bone. In the distal row of more lowly Tetrapods

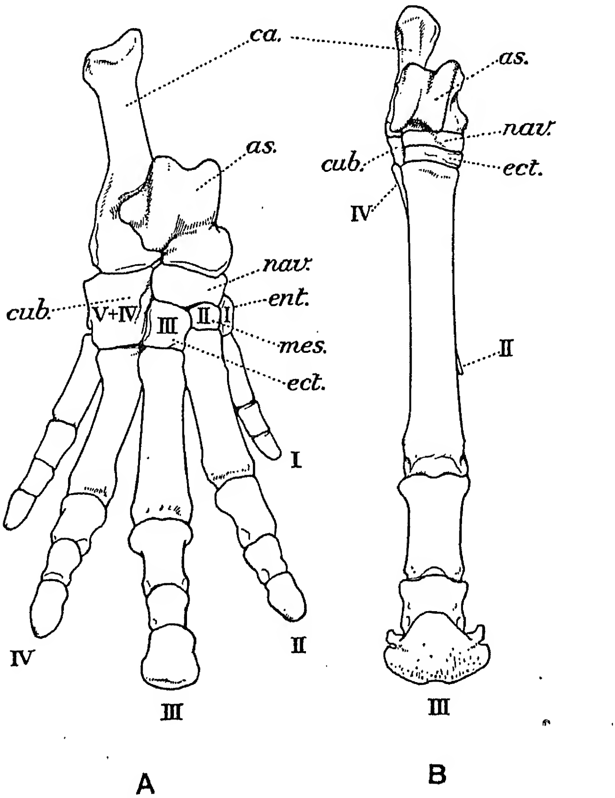



FIG. 7.—Skeleton of hind foot of horse (B) to compare with that of *Phenacodus* (A). Names of individual bones: *as.*, astragalus; *cub.*, cuboid; *ect.*, ectocuneiform; *ent.*, entocuneiform; *mes.*, mesocuneiform; *nav.*, navicular. The digits or toes are numbered with Roman figures.

are five separate bones, but in *Phenacodus* the fourth and fifth of these are fused into a single bone called the cuboid. Attached to this row of distal tarsals are five elongated bones called meta-

tarsals, and these at their distal ends support the phalanges or bones of the toes. In some of the mammals, as in reptiles and tailed amphibians, the body of the foot containing the metatarsals is placed flat on the ground (as in man), but more usually the heel is drawn up well off the ground, so that the weight is supported by the fore part of the foot. Such was clearly the case with *Phenacodus*.

Now if we turn to the hind-foot of the horse we notice the striking difference that it possesses only one toe, and that the weight is carried on the extreme tip of that toe, ensheathed in and protected by the hoof. The single toe is borne by a stout metatarsal, and that in turn is borne by the group of ankle bones of which the upper two are obviously astragalus and calcaneum, while the other three, from their relations with neighbouring bones, clearly raise the suspicion that they may really correspond to distal tarsal 3, navicular, and cuboid. We notice also on each side of the metatarsal a slender useless splint of bone (II. and IV.) which a comparative anatomist might well suspect of being also a metatarsal bone, in a relatively reduced condition.

It is not necessary to go into the details of the skeleton of the fore-foot of the horse, but it may be said that it too possesses only a single toe, and that its general arrangements show similarities and differences when compared with the fore-foot of other mammals closely corresponding with those shown by the hind limb.

At the present day the horse type (*Equus*), so far as truly wild species are concerned, is

restricted to the Old World, being represented by Przhvalsky's horse of Central Asia, the wild asses of Asia and Africa, and the two species of zebra. The troops of "wild" horses mentioned by travellers as occurring on the prairies of North America and on the Pampa of South America well on into the nineteenth century were not truly wild species: they were merely the descendants of domesticated horses introduced by European colonists. And yet curiously in comparatively recent geological times—during the early part of the Quaternary period—true wild horses, belonging to species differing only very slightly from the wild species of *Equus* existing to-day, abounded on the American as on the other great continents. How they came to die out is an interesting problem. It was not, in all probability, because of the general conditions of life becoming unfavourable to the existence of horses. That these conditions remained thoroughly favourable is indicated by the way in which horses survived and multiplied when introduced by the early colonists. The probability would appear to be rather that the original wild horses were exterminated by some protozoan microbe such as a Trypanosome. The power of trypanosomes to make a clean sweep of the horses over considerable tracts of country is, as I have learned by personal experience, demonstrated from time to time in South America by the epidemics of the exceedingly deadly trypanosome disease known as Mal de caderas.

As has already been remarked the fossil horses of early quaternary age differed but little from the horses of to-day, but when we pass back to the deposits formed in late tertiary times we find in

addition to small one-toed horses (Fig. 8, E) other creatures of what may be called the Hipparion type represented by the genera *Hipparion* and *Protohippus*. These were rather smaller than the typical horses (10-11 hands), but the most striking feature (Fig. 8, D) is that there is present on each side of the main digit a complete small toe instead of merely a slender splint bone. Although the small toe is complete it is not long enough to reach the ground, and consequently could not have been functional.

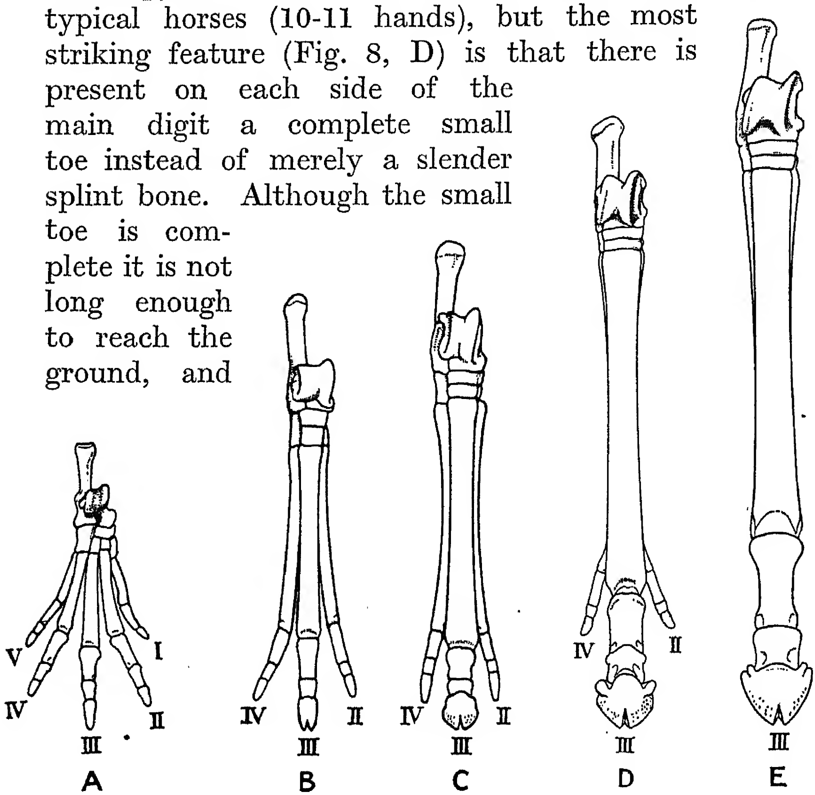



FIG. 8.—Illustrating the evolutionary history of the horse's foot as displayed by fossils. A, *Euprotogonia*—Lower Eocene; B, *Eohippus*—Lower Eocene; C, *Mesohippus*—Lower Oligocene; D, *Hipparion*—Upper Miocene and Lower Pliocene; E, *Pliohippus*—Upper Miocene and Lower Pliocene.

In the rather more ancient deposits belonging to the Oligocene period we find the genus *Mesohippus* (Fig. 8, C), a creature no larger than a sheep, in

which not only are there three complete toes present, but the side toes clearly reached the ground, and were therefore functional. Not only so, but in the case of the fore-foot we find on the outer side of the foot a slender splint bone which suggests a vestigial fifth digit.

In the deposits of the Eocene period the horses are represented by a number of small creatures no more than 12 or 13 inches in height, belonging to such genera as *Eohippus* of America and *Hyracotherium* of Europe. In the hind-foot of *Eohippus* (Fig. 8, B) the three toes are almost of the same size, while a little splint of bone on each side represents the remains of the first and fifth digits. In the fore-foot there is a complete fifth toe, though it is smaller than the other three, while even the first digit is represented by a slender splint.

When we reach such creatures as *Eohippus* we have got back from the highly specialized foot of the modern horse to a type of foot of a comparatively primitive, unspecialized kind, which differs but little from that possessed in early Eocene days by the primitive ungulates known as Condylarthra exemplified by the genus *Euprotogonia* (Fig. 8, A), and also by the larger *Phenacodus* (Fig. 7, A). In these the foot possesses the full number of five toes, but the middle one (III.), so situated as to take a larger share of the animal's weight, has become, in accordance with this, slightly stouter than the others, and in the case of *Phenacodus* a slight flattening of its terminal phalanx distinctly foreshadows the development of a hoof in place of the primitive claw.

It is clear that these palaeontological facts

when pieced together constitute an extraordinarily beautiful and absolutely convincing paragraph of evolutionary history, telling us how the remarkable one-toed foot of the modern horse has arisen by a process of gradual modification from the perfectly ordinary type of mammalian foot exemplified by *Euprotogonia*. We see how the supporting function became more and more concentrated in the middle toe, which in accordance with this underwent an increase in relative size, while on the other hand the side toes underwent a corresponding process of reduction. Thus in *Eohippus* the digits I. and V. have shrivelled away to small vestiges. In *Mesohippus* digits II. and IV. are undergoing a similar process of reduction, being quite slender as compared with the stout middle digit. In *Hipparion* and *Protohippus* the relative reduction of digits II. and IV. has gone a stage further, these toes no longer reaching the ground and having lost all their functional importance. Finally, in the horse (*Pliohippus* and *Equus*) these side toes have vanished away completely with the exception of the slender splint bones, hidden under the skin, and representing the remains of their metatarsals.

I have confined myself to the evolutionary history of the hind-foot, but I may say that fossil remains of the fore-feet tell precisely the same tale : only it is of interest to note that the fore-foot lags somewhat behind in its evolutionary progress—in correlation no doubt with its somewhat lesser functional importance in driving the body forwards.

As already mentioned, the high degree of specialization of the modern horse is also marked

in the structure of its teeth. Feeding as it does on harsh grassy vegetation, which wears down the teeth with great rapidity, it is necessary that the teeth should possess special arrangements to prevent their becoming rapidly useless through wear and tear.

What these arrangements are will be grasped most easily if we consider them first as they occur in a group of mammals other than the horses, namely the elephants.

In the extinct types of elephant known as Mastodons the crown of the grinder tooth (Fig. 9, A) projects in the form of strong blunt transverse ridges, each ridge composed of the normal tooth substance *dentine* (Fig. 9, *d*) covered with a layer of exceedingly hard *enamel* (*e*).

In the corresponding tooth of the modern elephant (Fig. 9, B) special provision has been made against wear and tear by an immense increase in the height of the crown. The transverse ridges are more numerous, and they have greatly increased in height so as to assume the form of thin parallel plates. These are so thin that their fragility would make them completely useless were it not that another modification has taken place—the deep intervening valleys having become filled up by a bony tissue known as cement (Fig. 9, B, *c*). The great crown of the tooth, built up of these thin plates embedded in the intervening cement, gradually wears down with use, but as it does so the enamel, owing to its being much harder than either dentine or cement, wears down less rapidly, and in consequence comes to project above the general surface so as to keep that surface irregular and therefore efficient for grinding the food.

Zoologists apply special technical terms to the two types of teeth exemplified by the grinders of the Mastodons and the modern elephant respectively: a low-crowned tooth like that of the mastodon is called *brachydont*, a high-crowned one like that of the modern elephant—*hypsodont*.

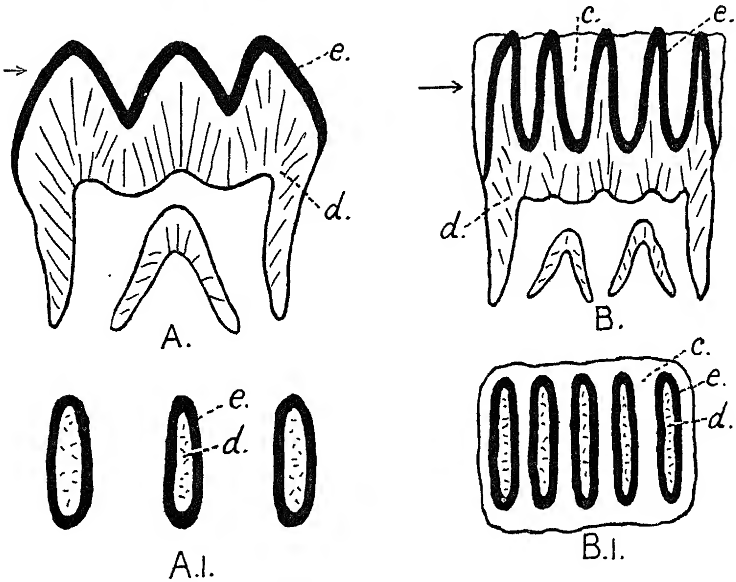



FIG. 9.—Structure of a grinder tooth (A) of a Mastodon and (B) of a modern elephant, as seen in longitudinal vertical section. The lower figures (A.1. and B.1.) represent the surface of the tooth when worn down to the level of the horizontal arrow. *c*, cement; *d*, dentine; *e*, enamel.

The evidence of fossils demonstrates that the highly specialized hyposodont grinder teeth of the modern horse have come into being by a process of gradual evolutionary change which has accompanied the modification of the limbs. In *Hyracotherium* the grinders are brachydont, the crowns projecting into low rounded knobs. In *Eohippus* the knobs have coalesced to form low

ridges. In the Miocene three-toed "horses" the ridges on the crown of the teeth are more pronounced, and in the genera *Protohippus* and *Pliohippus* not only have the ridges become much higher, but the valleys between have become filled in with cement. Finally, in the modern horse the tooth has a crown enormously tall in proportion to the fang or root, and the projecting ridges are so developed as to form when worn down a complicated and characteristic pattern. In order to keep the grinding surface at the proper level the wearing-down process is counteracted by a slow upward shifting of the tooth in its socket.

It will be clear, then, from what has been said, that as regards the three most striking peculiarities of the modern horse—its great size, its highly specialized one-toed limbs, its hypsodont teeth—the geological record has already yielded precise details of the evolutionary steps by which these peculiarities have gradually come into existence.

## The Evolution of the Elephant

As a second example of such evolutionary paragraphs provided by palaeontology we may take one relating to the Proboscidea—that remarkable group of mammals represented by the elephants of to-day. Apart from their great size, these creatures are characterized particularly by peculiarities in the structure of their head. The nose is drawn out into the long and flexible trunk. The great weight of the head necessitates an immense development of the muscles of the back of the neck to support it, and in order to provide the necessary increase

of surface for the attachment of these we find that the hinder part of the skull has greatly increased in height (Fig. 10, E). This increase in the height of the skull is by no means accompanied by a corresponding increase in its weight, for the bone, instead of being solid, is excavated by innumerable air-filled cavities communicating with the nose. The teeth of the elephant are greatly reduced in number as compared with those of ordinary mammals, but such as are present are of enormous size. In each jaw and on each side there are visible only one or two grinders; these are of the complicated structure described on p. 35; they are set obliquely in the jaw, and as each tooth becomes worn down it becomes slowly displaced forwards and eventually shed, while another tooth develops to take its place.

The only other teeth present are two greatly enlarged incisors, the tusks, long curved cones of dentine modified in its minute structure so as to have the great strength and elasticity so important for their efficiency as levers for uprooting trees and similar functions.

In Fig. 10 are shown a number of fossil skulls, which indicate how much light palaeontology has already succeeded in throwing upon the evolutionary history of the skull of the elephants. The upper figure shows the skull of a fossil mastodon of Upper Pliocene age, which is seen to have reached a height of development very similar to that of the modern elephants of to-day. It shows clearly the enormously exaggerated upper incisors (tusks), the great height of the back of the skull, the reduction in number of the grinder teeth to two on each side above and below, and their compensating increase in size.

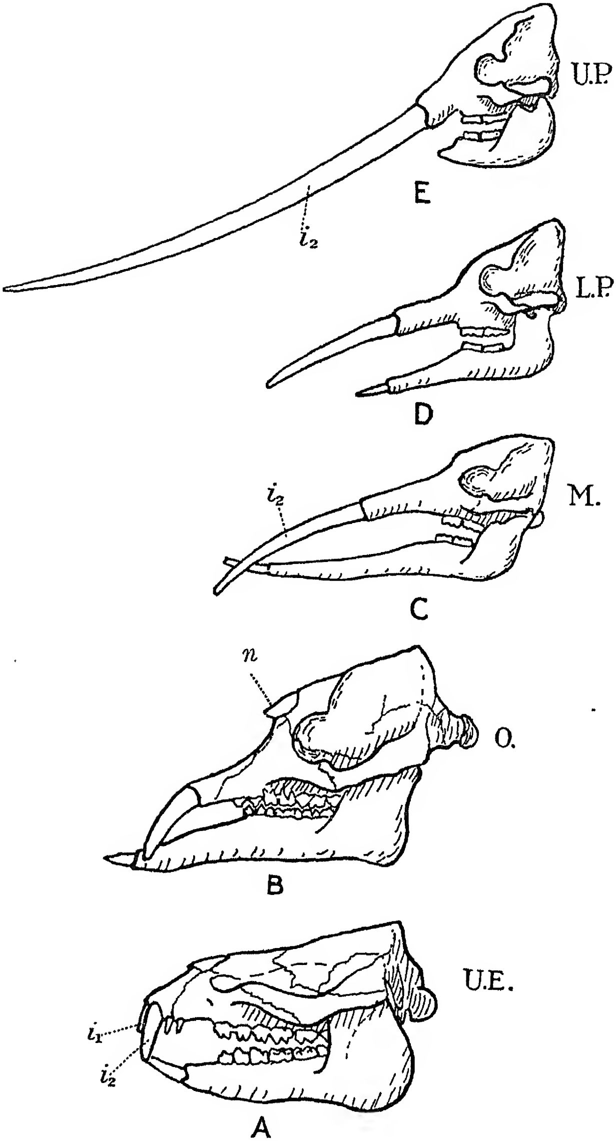



FIG. 10.—Illustrating the evolution of the elephant's skull. (After Andrews and Abel.) A, *Moeritherium*—Upper Eocene; B, *Palaeomastodon*—Oligocene; C, *Tetrabelodon* (or *Bunolophodon*) *angustidens*—Miocene; D, *Tetrabelodon* (or *Tetralophodon*) *longirostris*—Pliocene; E, *Mastodon* (or *Anancus*) *arvernensis*—Pliocene. $i_1$ and $i_2$, first and second incisor teeth of upper jaw; $n$, nasal bone.

*Note.*—The figures are not drawn to scale. In actual size the skulls show successive increases in size from A to E.

The lower jaw shows a characteristic shortening inasmuch as it projects forwards hardly at all in front of the region of the grinder teeth.

In the older (Lower Pliocene) type of mastodon, shown in D, the incisor teeth are seen not to be confined to the upper jaw, a pair of lower incisors of small size being present; and in correlation with their presence the lower jaw is prolonged forwards.

In the Miocene *Tetrabelodon angustidens*, shown in C, not only are lower incisors present, but it is clear from their shape that they could be used for biting or seizing, probably biting against a hard pad in the roof of the mouth prolonged on to the snout. In both this and the mastodon last mentioned the jaws, both upper and lower, are seen to be greatly prolonged forwards.

In the Oligocene *Palaeomastodon*, shown in B, the incisors are much less aberrant in form, and this applies to the skull as a whole, the short nasal bones (*n*), for example, projecting forwards over the nostrils as they do in normal mammals. The grinder teeth, instead of being unusually few, number six in the upper and five in the lower jaw on each side.

The Upper Eocene *Moeritherium* (A) was a much smaller creature—about the size of a tapir—and its skull was very much that of an ordinary ungulate. Here and there, however, appear features which clearly foreshadow those of the later Proboscideans. In particular, the second incisor teeth in both jaws are enlarged, while in the lower jaw the front portion carrying the incisors is prolonged forwards. The grinder teeth are six in number, and their crowns carry rounded knobs arranged in pairs

crosswise, each pair clearly foreshadowing the transverse ridges of the mastodons. The nasal bones are short, lying behind a large nasal opening, which suggests that an incipient trunk like that of the modern tapir may have been present.

If, then, we read Fig. 10 from below upwards, we see in it a perfectly clear little paragraph of evolutionary history, leading from comparatively small unspecialized mammals to creatures of much greater size provided with much enlarged, forwardly projecting tusks in both jaws, and these in turn to the regular elephant type, in which the lower incisors and the portion of jaw carrying them have again shrunk away to nothing, while the upper incisors have undergone the enormous development characteristic of the typical elephants.

The two instances I have summarized—that of the horse and that of the elephant—are, I think, amply sufficient to give an idea of the wonderful paragraphs of evolutionary record already provided for us by palaeontology. I need not cite any more of such paragraphs, but I may say there are many others, and their number is undergoing continual increase as investigation proceeds, so that the future holds out an unlimited vista in the way of additions to evolutionary knowledge which will come to us from palaeontology.

It is, however, not only by such consecutive paragraphs that palaeontology contributes to evolutionary history. From time to time it divulges to us links hitherto missing which by their intermediate character serve to join up types of animal that appeared to be isolated. Thus it has provided in *Archaeopteryx*, from the Jurassic lithographic stone of Bavaria, a creature which links up the birds

to the reptiles. Of about the size of a crow, *Archaeopteryx* is clearly a bird in its general features, and there are distinct remains of wing and tail feathers. Yet in various details it is by no means an ordinary bird. In its upper and lower jaws are teeth. Its fore-limb, though clearly a wing, is not so highly specialized as that of the modern bird. The hand—degenerate in the modern bird, its three digits (I., II., III.) more or less fused together to serve merely as a support for the wing feathers—has its three fingers well developed and freely movable, each one provided with a strong claw. Its tail, instead of being reduced to a short stump bearing a fan of feathers as in the modern bird, is slender and tapering like that of a lizard, as long as the rest of the body and head, and carries the flat tail feathers in a row along each side. The bones of the trunk—vertebrae, breast-bone, and ribs—which in the modern bird are joined together to form an elastic cage-like arrangement, of importance in its peculiar method of breathing, do not show this peculiarity, but are still freely jointed to one another as in ordinary terrestrial vertebrates.

Again in the deposits belonging to the close of the palaeozoic era have been found a number of creatures which are so clearly intermediate in character between amphibians and reptiles that doubt arises whether it is correct to include them in the one of these groups or in the other.

Palaeontological research has also yielded important data regarding the evolutionary history of particular portions of the skeleton. Thus, for example, the delicate bony rays that support the fins of modern fish are shown to be metamorphosed scales, for some of the ganoid fishes of late palaeozoic

age show every transition between the ordinary scales of the body and the slender drawn-out rays of the fin.

Finally, if we make a general survey of the fossil remains yielded by the various geological formations, we see clearly, as one formation succeeds another, that the assemblage of animal forms becomes more and more like that which is to be found alive on the earth to-day, a gradual process of evolutionary change taking place.

If, however, we examine more thoroughly this record of the animal population through the ages, another and astonishing fact becomes apparent, namely, that the existing palaeontological record, covering though it does inconceivably vast periods of time, yet dates only from a period that seems comparatively close to the present day when considered in relation to the whole period of evolutionary time; for we find that so early as the epoch marked by the most ancient fossiliferous rocks (Pre-Cambrian and Lower Cambrian) there had already come into existence groups of animals (Crustaceans, Trilobites, Brachiopods, bivalve Molluscs) that had reached such a comparatively high grade of organization as to leave us no escape from the conclusion that these rocks represent a period in evolutionary time incomparably farther removed from the actual dawn of life upon this earth than from the present day. In fact, the entire palaeontological record, as we know it, which has yielded up so much fascinating information, turns out to represent merely the closing pages of evolutionary history. All except these closing pages has,

so far as is known, been destroyed or obliterated by the long-continued destructive processes to which the more ancient rocks have been subjected.

The contributions of palaeontology to evolutionary history are so splendid and so entrancing that there is considerable danger of the critical faculty being lulled to sleep when regarding them instead of being particularly wide awake as it must needs be if false conclusions are to be avoided. Some of the most obvious pitfalls lying in the way of the unwary palaeontologist are these. He may forget at times that his material is representative usually of only a single organ system—the skeleton—and very often of only a single more or less imperfect fragment. Now those whose work is concerned with the structure of existing animals have learned to recognize that the reliability of their conclusions is apt to be roughly proportional to the broadness of the evidence on which they are based. In puzzling out morphological problems such workers like to be fortified by the evidence of different organs of the body and of numerous specimens, for they know by experience how great otherwise is the liability to error. The sound palaeontologist is particularly careful never to lose sight of the limitations of this kind under which he suffers when tempted to draw theoretical conclusions from his facts of observation.

Another pitfall is that of taking the discovery of a fossil as marking the first appearance of a particular type in evolutionary time. For example, it might be stated that birds made their first appearance in the Jurassic times marked by the deposits of lithographic stone from which *Archaeopteryx* has been obtained. As a matter of fact only two or

possibly three specimens of *Archaeopteryx* are so far known, and these are commonly referred to distinct species. It is clear that all we are really justified in concluding is that these specimens represent a type of creature which in all probability existed in enormous numbers, and possibly in many different species, at the date of deposition of the Solenhofen stone. As to how much earlier it made its first appearance, all that we are justified in stating is that we have no evidence.

Again it is necessary to exercise great caution before concluding that fossils in consecutive strata represent a true ancestral series. Thus it is not justifiable to speak of any one of the fossil horses referred to on pp. 32-34 as being actually ancestral to the modern horse. All we can say, with safety, is that each represents an ancestral type of structure. There can be little doubt that each of these types was, in the days of its prosperity, represented by several, probably by many, species, and which of these was the direct ancestor of the modern horse is not determinable.

It is also necessary to be very careful in translating palaeontological discoveries into terms of time. One often comes across, in popular writings, statements that such and such a type of creature came into existence about so many millions of years ago. Such statements are, for the reasons that will have been gathered from Chapter I., of no scientific value, and should be avoided as being liable to arouse distrust, often quite undeserved, in the general reliability of palaeontological research.

A species of error of a more dangerous kind, because of the particularly elusive form in which

it is apt to occur, is that of depending too implicitly upon the general principle that fossils obtained from a sequence of geological formations represent a corresponding sequence in evolution. As a general principle this is of course quite true: but in exceptional cases it is liable to break down. What I regard as an instructive example of this is afforded by the known fossil Dipnoi or lung-fish. Fig. 11 B, C, D, and E represent types of lung-fish obtained from the Lower Carboniferous, younger and older parts of the Upper Devonian, and the Lower Devonian respectively, and many palaeontologists, following Dollo, accept these as representing an evolutionary sequence. If, however, we ignore the rocks in which these fossils were found and regard them from the point of view of physiology, of comparative anatomy, and of embryology, we see that in the main feature in which they differ, namely, the arrangement of the median or unpaired fins, we have to admit that of the four types E is the most highly and B the least highly evolved. It is, for example, one of the most regular features of fish development that the tail is at first straight, pointed, and symmetrical (protocercal), as in A, but that, as the evolution of the individual proceeds, the tail develops an upward tilt, and the originally continuous and uniform median fin, becoming exaggerated at points where it is most effective and dying away at intermediate points, becomes resolved into a series of separate dorsal and ventral fins, as in E. Such is the process that can be actually seen to take place in the evolution of the individual during its development, and as it is in complete accord with physiological and comparative anatomical considerations, it would require

weighty evidence to render probable that the normal course of evolution has been reversed in

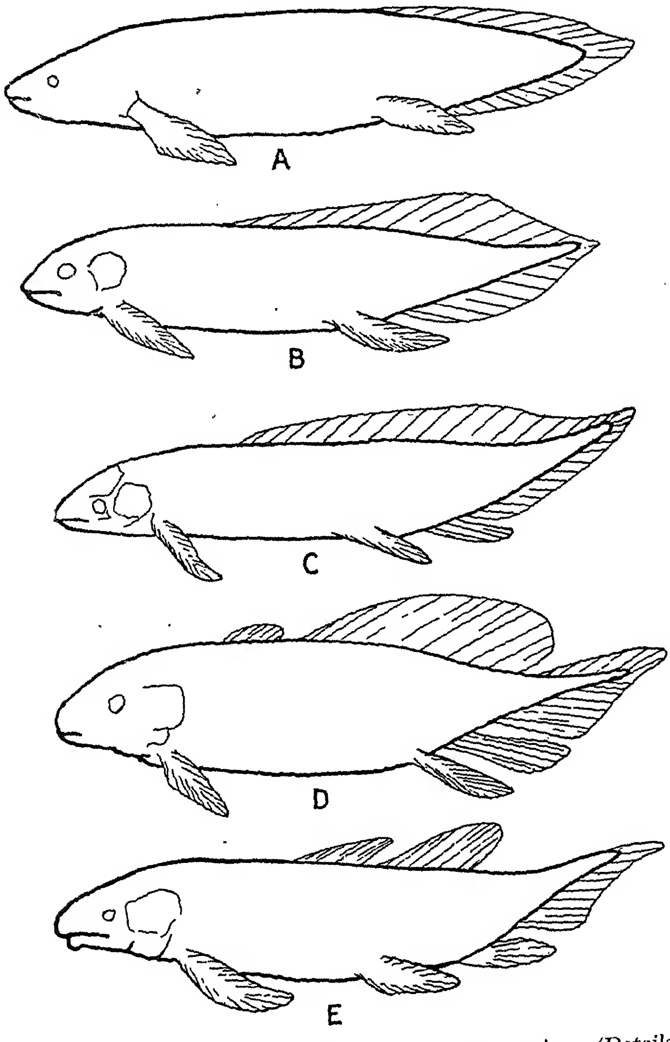



FIG. 11.—A probably misleading palaeontological series. (Details after Traquair: sequence according to Dollo.) A, *Ceratodus*—present day; B, *Uronemus*—Lower Carboniferous; C, *Phaneropleuron*—Upper Devonian; D, *Scaumenacia*—Upper Devonian; E, *Dipterus*—Lower Devonian.

the particular set of fish shown in Fig. 11. I do not put it more strongly than this, for there is no doubt that occasionally evolutionary progress is reversed, particular features undergoing reversion towards an earlier evolutionary condition.

The fact that the structurally less highly evolved types represented in the upper part of the figure have not as yet been discovered in the older formations is, to my mind, sufficiently explained by the imperfection of the record. As a matter of fact, there is always a greater probability of more powerful swimmers, such as those in the lower part of the figure, being preserved as fossils, for the double reason that they alone live among the strong currents that facilitate rapid entombment, and that they are more apt to crowd together in shoals.

### BOOK FOR FURTHER STUDY

LULL. *Organic Evolution.*

# CHAPTER IV

## COMPARATIVE ANATOMY AND THE NATURAL GROUPING OF ANIMALS

THE two preceding chapters had as their object proof of the fact of secular or racial evolution. This chapter will serve to indicate the flood of light that is cast by the theory of evolution upon the structure of animals as revealed in the science of comparative anatomy; the fact of its being so effective in this becomes in turn a strong corroboration of its own truth.

When a broad view is taken over the whole expanse of the animal kingdom the predominant impression is perhaps that of its endless diversity. Then amid this diversity a certain order becomes apparent. The multitudinous individuals are seen to be linked together by their resemblances into definite kinds or species. Species are in turn linked by the possession of common characteristics into larger groups or genera, these in turn into larger groups, and so on—the various groups of any particular order being united by their resemblances and demarcated by their differences. In short, there exists in nature a natural classification of animals, a grouping together into assemblages of various orders of importance by their structural resemblance. The species of a genus are united by a common plan of structure, so also the genera of a

family, the families of an order, and so on. Now it is clear that this natural classification of animals is just what we should expect as a result of evolution—the higher degrees of resemblance being expressive of closer blood relationship, the lower degrees of resemblance being expressive of less close relationship.

The resemblances just alluded to are concerned with the visible form and structure of the body, but it may appropriately be mentioned at this point that modern research has brought to light the important fact that such visible resemblances are accompanied by others of an obscure and invisible kind apparently chemical in their nature. It is found that alien blood injected into the body of a living vertebrate has in many cases a highly poisonous effect, bringing about haemolysis or destruction of the red blood corpuscles of the animal operated upon. This toxic effect is, however, not produced when the blood injected is taken from an animal of the same species, or of a species similar in its general structure and therefore close to the injected animal in the scheme of zoological classification; the toxic effect is associated, in other words, with dissimilarity in the general structure of the two animals and is expressive, we may take it, of a corresponding dissimilarity in the fluid of their body—the internal medium which will be referred to later (p. 267).

It is possible to get a quantitative idea of the degree of such dissimilarity by a method of experiment developed particularly by Nuttall.[1] Small quantities of blood serum of an animal A are injected repeatedly at intervals of a couple of days

[1] See his *Blood Immunity and Blood Relationship.*

into the blood of a rabbit, and after the lapse of about a week the serum of this rabbit is found to have developed the power of causing a cloudy or milky precipitate when a small quantity is added to clear blood serum taken from another individual of the same species as A. The reaction, however, is not restricted absolutely to animals of that same species: it takes place also in individuals belonging to neighbouring species in the scheme of classification, but diminishes in intensity as the animals experimented on are farther and farther away from A in the classificatory scheme. Consequently the degree of activity of the reaction—as shown by its intensity and its rapidity—may be taken as affording an index of the degree of similarity in the constitution of its body fluid between the animal experimented on and the animal A. The reader will notice the important implication in what has just been said; namely, that, when once it is firmly established that the resemblances between animals are expressive of evolutionary relationship, then the degree of closeness of that relationship between two species of animals may be said to be *measurable* by the degree of activity of their serum reaction.

Another important body of evidence is afforded by organs of the animal body which in accord with differences of function show a striking dissimilarity in appearance, but which when more deeply investigated are found to possess a fundamental similarity in structure.

A good example is seen in the fore-limb or pectoral limb of a dog, a whale, a bat, and a man. These organs are conspicuously different in appearance, as indeed we might expect, seeing that their

functions—running, swimming, flying, grasping—are so unlike. We should naturally expect their internal structure to be similarly unlike. It is obvious that an engineer given the problem of designing the best type of mechanism for carrying out these very different functions would not adopt a common plan for them all; but yet in actual fact the internal structure of these organs is found to be arranged on a common plan. This is clearly brought out in Fig. 12, which shows how the skeleton of these so different forms of limb is built up out of corresponding sets of elements, the differences being due mainly to the different degree of development of the corresponding bones in the different cases. Obviously this is exactly the state of affairs which we should expect had all these limbs evolved out of a common ancestral type.

Another good example is afforded by the organs associated with the mouth in such different insects as the cockroach, the bee, the mosquito, and the butterfly. These creatures feed in quite different fashions—the cockroach nibbles its solid food, the bee sucks nectar and licks up pollen, the mosquito makes an incision into the substance of an animal or plant and through it sucks up blood or sap, the butterfly sucks up the nectar of flowers. The apparatus by which the feeding process is carried out looks, as we should expect, very different in these different insects. The bee possesses a hairy tongue for licking up pollen, combined with a tubular channel for sucking nectar; the mosquito possesses a wonderful little case of surgical instruments by which it cuts through the skin and draws up the blood; the butterfly possesses a long tubular proboscis—carried, when not in use, coiled

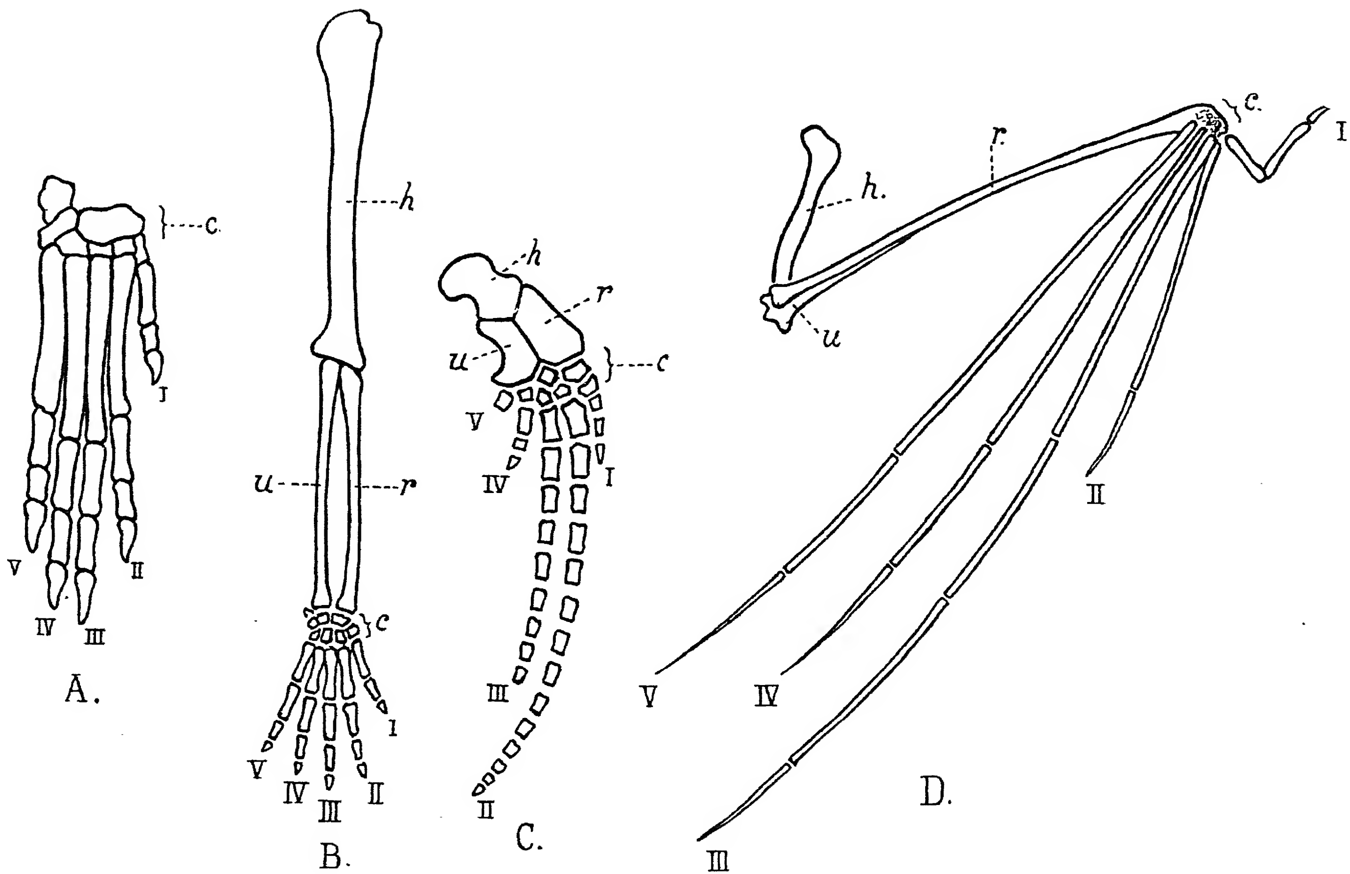



FIG. 12.—Illustrating the general arrangement of the bones in the fore-limb of a dog (A), a man (B), a whale (C), and a vampire bat (D). *c*, carpus or wrist ; *h*, humerus ; *r*, radius ; *u*, ulna. The digits are indicated by Roman numerals.

into a tight spiral under the head—which it can lower far down into the flower-tube to draw up the nectar. And yet examination in detail (cf. Fig. 13) shows that such highly specialized feeding apparatuses are made up of the same set of component parts, merely modified in detail in specialization for the different functions. This is at once understandable if they have all been evolved

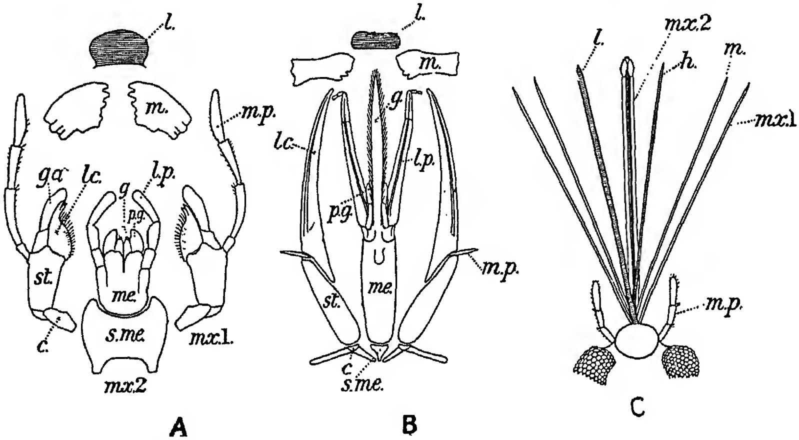



FIG. 13.—Mouth parts of insects. (From Graham Kerr's *Zoology for Medical Students.*) A, Cockroach (*Periplaneta*); B, Bumble-bee (*Bombus*); C, Mosquito (*Culex*). Names of parts: *c*, cardo; *g*, glossae or ligula; *ga.*, galea; *h*, hypopharynx; *l*, labrum; *lc.*, lacinia; *l.p.*, labial palp; *m*, mandible; *m.p.*, maxillary palp; *me.*, mentum; *mx.*1, first maxilla; *mx.*2, second maxilla (labium); *p.g.*, paraglossa; *s.me*, submentum; *st.*, stipes.

out of a common ancestral set of mouth parts, but otherwise is quite incomprehensible.

The type of argument that has just been indicated may also be used in converse fashion. Fig. 14 shows the skeleton of the wing in flying vertebrates belonging to three different groups—reptiles (Pterodactyl—A), birds (B), and mammals (bat—C). It will be seen that the wing skeleton is obviously built up of the same set of bones in the

three cases, but that these have been fashioned in quite different ways to form the complete skeleton. In the pterodactyl the wing was a thin membrane supported along its outer edge by the enormously enlarged fifth finger (A, V)—corresponding to the little finger of man.

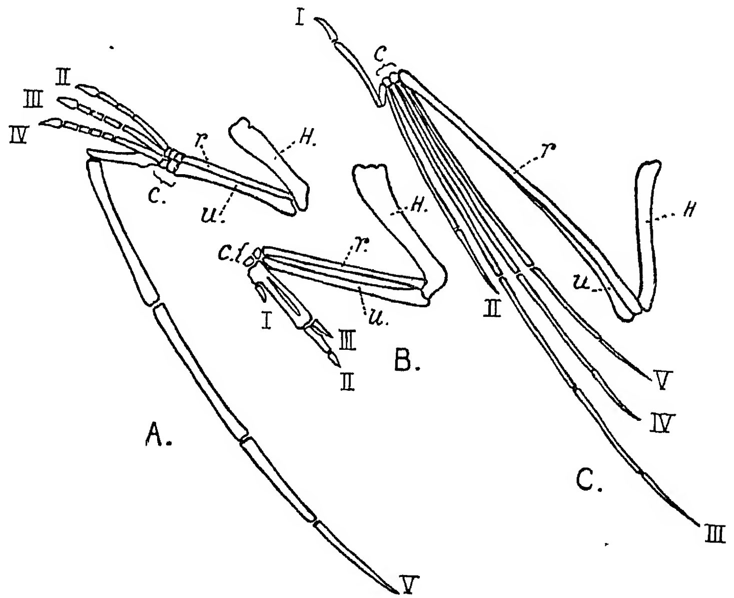



FIG. 14.—Illustrating the general arrangement of the bones of the wing in a Pterodactyl (A), a bird (B), and a bat (C). *c*, carpus ; *H*, humerus ; *r*, radius ; *u*, ulna. The individual digits are numbered with Roman figures.

In the bird the main expanse of the wing is formed by the feathers, the quills of which are firmly fixed at their bases to the bones of the fore-arm and hand, and the hand, having only this simple supporting function to perform, is correspondingly simple in structure, the three digits present (I., II., III.) being, as already mentioned on p. 42, more or less degenerate and fused together.

In the bat the wing is a thin membrane, as it was in the pterodactyl, but in this case the membrane is spread out by the greatly prolonged finger-bones, more especially those of digits III., IV., and V., which support it like the ribs of an umbrella.

The facts just mentioned are again in absolute accord with the idea of evolution. The skeleton of the three types of wing consists of the same elements, because the three types of wing have all evolved out of the fore-limb of the terrestrial vertebrate. There are, however, striking differences in detail, because the three types of wing have evolved quite independently of one another from the ancestral type of limb.

## Vestigial Organs

Another important body of evidence is afforded by the occasional organs which occur in the animal

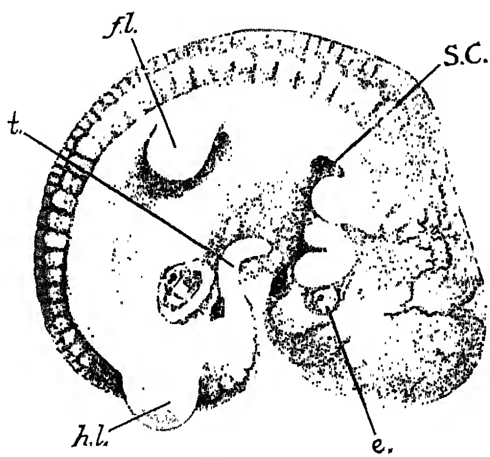



Fig. 15.—Young human embryo seen from the right side. (From Assheton, Hill and Wilson, *Embryology*.) *e*, eye; *f.l.*, fore-limb; *h.l.*, hind-limb; *S.C.*, region of gill-clefts; *t*, tail.

body without their presence having any obvious justification in the way of work which they perform.

For example, man possesses a useless little tail, conspicuous enough in the embryo (Fig. 15), but consisting after birth only of a few bones tucked away out of sight beneath the skin (Fig. 16), except in the case of very rare abnormalities (Fig. 17). Again, for a time during his embryonic life, man possesses a coating of fur all over his body.

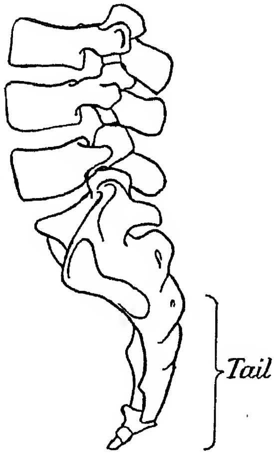



FIG. 16.—Lower end of vertebral column of man, showing the last three separate vertebrae and the sacrum tapering off into the tail or caudal vertebrae.

Both of these peculiarities are obviously at once understandable on the evolution theory, which tells us that man is descended from ordinary mammals which ran on all-fours and possessed a functional tail; which had not yet taken to wearing clothes and consequently had not yet lost the natural covering of fur.

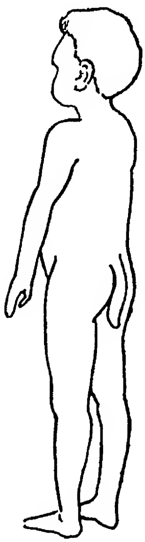


FIG. 17.—Abnormal ten-year-old boy with visible tail. (After Wiedersheim.)

On the shoulder-blade of man there is present an apparently meaningless and useless projection called the coracoid process, from its fancied resemblance to the head of a crow. This peculiarity is again explained by the evolution theory, which shows us that the coracoid process is simply the

shrunken remains of what in the lower types of terrestrial vertebrates is an important structure—the coracoid bone—a bony strut which serves to hold out the shoulder-blade in its proper position in spite of the pull of certain muscles which tend to draw it forwards on to the chest.

Another typical case of a useless organ is the slender splint bone on each side of the horse's foot, which the evolutionary interpretation of comparative anatomy tells us is the remains of a toe

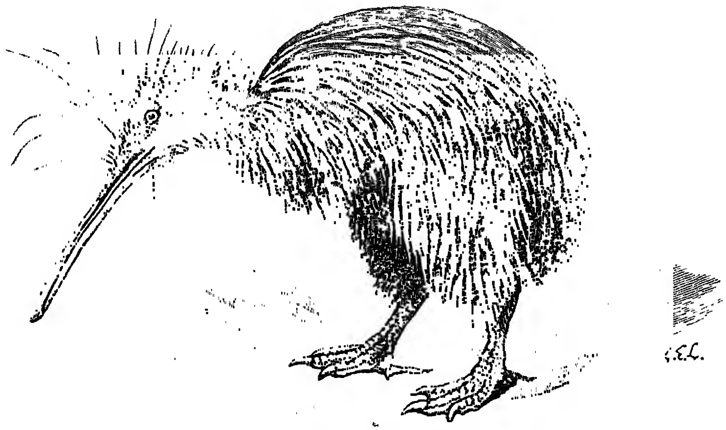


Fig. 18.—The Kiwi—*Apteryx*.
(From Evans, *The Cambridge Natural History*.)

present in a less highly evolved stage. In this case, as already indicated, palaeontology comes to our aid, and demonstrates to us by actual specimens that this is the case.

Another good example is afforded by that remarkable New Zealand bird, the Kiwi (*Apteryx*) (Fig. 18), which runs rapidly, but has no power of flight. Its body is covered with a thick coating of almost hair-like feathers. By feeling with the finger amongst these feathers one can detect the

presence of a miniature wing hidden amongst them. It is so small as to be absolutely useless, although it is asserted that the kiwi tries its best to tuck its bill under it when it goes to sleep!

This wing of the kiwi would have to be regarded merely as a mysterious absurdity were it not for the evolution theory, which tells us how the kiwi —highly specialized for running about on the ground — is an evolutionary development from ancestors which were ordinary birds possessing wings for the purpose of flight.

The lung of snakes affords another interesting example. In certain snakes there is a large actively functional right lung and a small comparatively useless left lung. The evolutionist would suggest as the meaning of this that the ancestors of snakes possessed, like normal air-breathing vertebrates, a pair of lungs—right and left—approximately equal in size, but that in correlation with the lengthening of the body as it assumed the typical snake form the left lung had undergone a gradual reduction in size. He would point out that in some snakes, such as the ordinary viper, a still further stage in the evolutionary process has been reached in which the left lung has disappeared altogether, leaving only a single — the originally right—lung.

Evolution thus provides a clear explanation of the presence of the small comparatively useless lung in those snakes in which it occurs. That this explanation is a correct one is confirmed by embryology, which shows us that the lopsided arrangement of the lungs is preceded by an earlier stage in development in which the two lungs are equal in size.

## Evolutionary Series

As a last example of the kind of evidence given by comparative anatomy we may refer to those cases where a number of types of animals differ from one another in such a way as to be capable of arrangement in a more or less regular series interpretable as illustrating a sequence of stages in evolutionary modification.

In the Mediterranean and other warmer seas there is occasionally encountered swimming sluggishly "upside-down" the curious creature *Pterotrachea* shown in Fig. 19, E. Measuring up to about 12 inches in length, its body is absolutely colourless and transparent except the little hump on its back. It has a long snout bent downwards, with a pair of complicated eyes at its base, and on its ventral side is a flat fin (*f*1) with which it swims about back downwards. Its general appearance is altogether peculiar, and it is necessary to investigate the details of its anatomy before it becomes apparent that it is really to be classified with the great group of Mollusca or shell-fish.

Peculiar as it is, it is now known that *Pterotrachea* is joined up by a chain of intermediate links with much more ordinary looking molluscs.

The first of these links is *Carinaria* (Fig. 19, D). Not unlike *Pterotrachea* in its general appearance, it has a less prolonged snout: beside each eye there projects a pointed tentacle: the fin has upon its posterior edge a sucker by which the animal can hang on to a floating log:[1] the most striking difference, however, is in the hump, which is here of relatively

[1] A similar sucker occurs in the male *Pterotrachea* but not in the female.

larger size and is protected by a distinct though fragile shell (*s*), shaped like a "Cap of Liberty" reversed, with its tip tilted backwards.

The next link is *Atlanta* (Fig. 19, C). The fin is differently shaped and the sucker is larger in proportion. The hump is much larger, is coiled in a spiral, and is enclosed in a spiral shell with a flat keel round its circumference. The shell here is large enough to form a protective house into which the whole animal can be drawn, the mouth of the shell becoming blocked by a flat horny plate or operculum (*op.*).

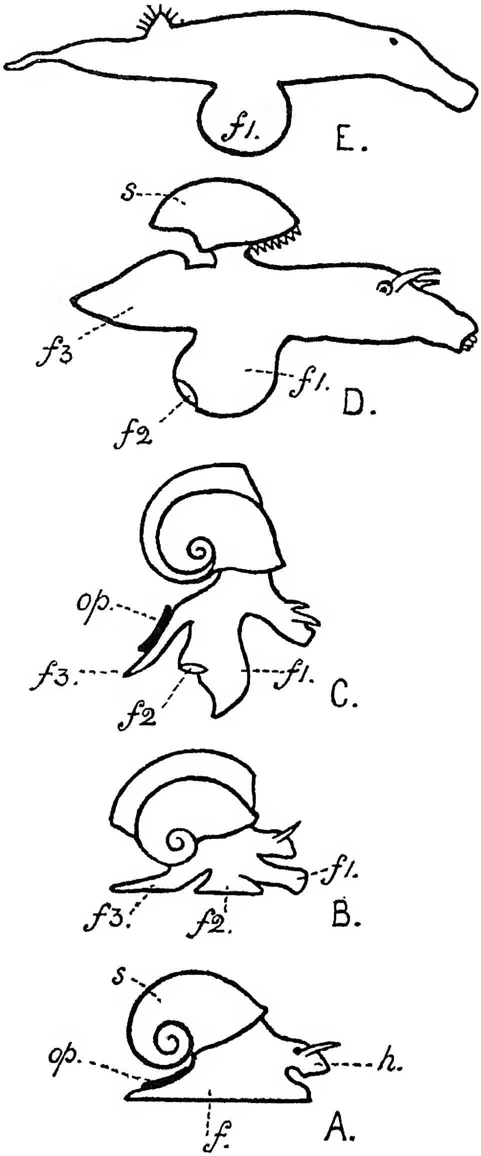



FIG. 19.—Heteropoda—an "evolutionary series". A, Diagram of an ordinary Gasteropod mollusc; B, *Oxygyrus*; C, *Atlanta*; D, *Carinaria*; E, *Pterotrachea* (female); *f*, foot; *h*, head; *op.*, operculum; *s*, shell.

The last link (*Oxygyrus*, Fig. 19, B) shows as its main difference that the fin, the sucker, and the part of the body carrying the operculum are in line with one another and are clearly recognizable as being simply the well-known foot upon which any ordinary snail or gasteropod creeps (Fig. 19, A).

Here, then, we have a typical series which, otherwise meaningless, teaches us in the light of the evolution theory how *Pterotrachea* is really a gasteropod or snail-like mollusc, which has become specialized in relation to a pelagic habit, the foot upon which it originally crept becoming divided up into a front part (*f* 1) which serves as a fin, a middle part (*f* 2) which either disappears (female) or becomes reduced to a small sucker (male), and a hind part (*f* 3) which for a time carries the operculum but later becomes simply merged in the body. The heavy shell—a valuable protection to the creeping snail—persisted for a time in the pelagic descendant, weighting the body and causing it to assume the upside-down position, but gradually became reduced and at length disappeared, the creature now depending for protection mainly upon the inconspicuousness due to its colourless transparency.

As another series we might take the chain of links which connects one of the more highly developed insects, such as a cockchafer beetle, with the simple marine worms or annelids.

In Fig. 20, A, we see a fairly typical marine worm (*Hesione*). It has an elongated body, from the sides of which project a series of crude stump-like legs (parapodia). In Fig. 20, B, is shown a very simply organized arthropod, *Peripatus*, which occurs in various isolated localities scattered over the warmer parts of the world. In shape not unlike A,

its legs or appendages show a greater complication of structure, inasmuch as each one is provided at its tip with a definite clawed foot. Further, the two front pairs of legs are curiously different from the others—the front pair being enclosed within the mouth opening, and serving as jaws, while the second pair serve as squirts by which a sticky

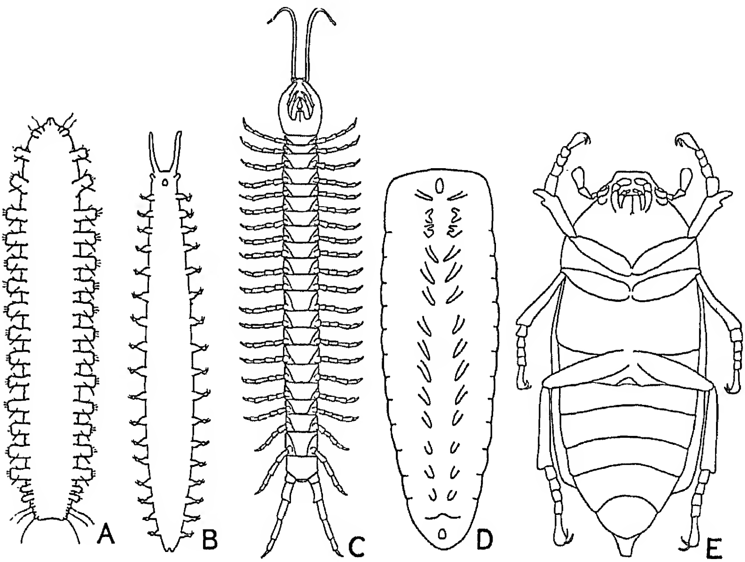



FIG. 20.—Annelid and arthropods as seen from the ventral side. A, an annelid worm (*Hesione*); B, *Peripatus*; C, centipede; D, early stage in the development of beetle; E, adult beetle (*Melolontha*).

slime can be projected at small insects and used as a means for their capture. In C is shown a centipede, in which the body is again elongated and worm-like. The surface layer of the skin has become stiffened to form a protective armour, which, in order to retain flexibility, is divided by numerous joints. The legs are here still more complicated than in *Peripatus* and are

jointed like the body. Further, the three front pairs differ greatly from the others and are used in connexion with feeding—the first pair being strong jaws, while the third pair are large poison claws by which the prey is killed. The last two figures are insects (Cockchafer), D representing a young stage (embryo) and E an adult. In the latter the body is not worm-like, but is short and squat, and divided up into three distinct regions, the head, thorax, and abdomen. On the abdomen no legs are present, on the thorax are three pairs of legs, more slender, more complicated in structure, and more efficient than those of the three preceding types. In the neighbourhood of the mouth are three pairs of appendages quite unlike the ordinary legs and used in feeding (cf. Fig. 13, p. 54). If, instead of the adult insect, we examine the young stage, shown in Fig. 20, D, we find a condition in some respects intermediate between that of the adult and that illustrated by A, B, and C—for the body is not yet subdivided into its three regions, and the abdomen is not devoid of appendages, but is provided with leg stumps like the parts of the body farther forwards.

If we now turn the light of the evolution theory upon the series of creatures just described, we see that the idea at once suggests itself that the modern insect has gradually evolved from an annelid-like ancestor by stages resembling in certain features the *Peripatus*, the centipede, and the insect embryo of to-day.

The value of such series is that they show how highly specialized and peculiar types of animals may be linked up with less highly specialized, and they fit in readily with the evolution theory, being

interpretable on that theory as illustrating so many steps in the evolution of the more specialized from the less specialized. A word of warning is necessary at this point. It must not be supposed that any species of creature pictured in one of these serial figures is to be regarded as itself the evolutionary ancestor of those shown in the later figures. As a matter of fact, no species of animal existing on the earth to-day is to be regarded as the ancestor of any other presently existing species. To suppose this would imply that evolution had stood absolutely still in its particular case. All that we mean is that each of these links in the series represents roughly a probable evolutionary phase that was passed through. Had we before us the actual ancestral form belonging to that evolutionary phase we should no doubt find that it differed quite perceptibly in superficial details from that figured.

# CHAPTER V

## THE GEOGRAPHICAL DISTRIBUTION OF ANIMALS, AND GENERAL CONCLUSION AS TO THE FACT OF EVOLUTION

A SECTION of zoological science which has to be specially noted in any book on Evolution is that which deals with what is sometimes called Zoo-geography—the study of the resemblances and differences between the fauna, or animal population, of the various regions of the world. Every one knows that there are striking differences between the faunas of different regions. Every one knows also that the differences between different faunas have a relation to the physical environment. We find one kind of fauna in the sea, another in fresh water; one in a rapidly flowing stream, another in a swamp; one in a luxuriant forest, another in an arid desert; one in a steaming tropical plain, another amid snowy mountain peaks. But if we look a little more deeply into the matter we find that there are other factors at work than mere differences in environment. For example, we might choose three localities bearing the closest resemblance in their environmental conditions but situated one in Queensland, one in Africa, and one in South America. Were only environmental factors at work we might expect

the fauna to be identical in the three cases, but we find, as a matter of fact, that under a certain amount of superficial resemblance there exist deep-seated differences.

In the African locality the fauna might include mammals such as antelopes, giraffes, camels, zebras, lions, leopards, elephants, apes; birds such as ostriches and honey-guides; and the lung-fish *Protopterus*. In the South American locality not one of these would occur, but there might be found opossums, armadillos, sloths, ant-eaters, peccaries, llamas, pumas, and jaguars; birds such as rhaeas, humming-birds, toucans, tanagers; the lung-fish *Lepidosiren*.

In Queensland again none of these would be found. The native mammals would all belong to the egg-laying Prototheria (Monotremes), or to the pouch-bearing Metatheria (Marsupials). Instead of ostriches or rhaeas there would be emus; instead of *Protopterus* or *Lepidosiren* the lung-fish *Ceratodus*.

On the other hand, we might select within the limits of one of these continents a number of localities as different as possible from one another—the snowy mountain-tops of the Andes, the steaming swamps of the Chaco, the bleak plains of Patagonia, the luxuriant tropical forests of Brazil. Nothing could be less alike in the way of terrestrial conditions, but yet when we examine into their animal populations we find that all through these there runs a deep-seated unity as striking as was the diversity in the three other cases.

When a general survey is made of the large body of facts of the kind indicated, certain main principles are seen to emerge. It becomes apparent

that the resemblance between the faunas of two different localities is correlated with the degree of their accessibility one from the other. If the degree of accessibility is high, if animals can pass readily from the one to the other, their faunas tend to be alike. If, on the other hand, the degree of accessibility is low, if they are separated by barriers which form obstacles in the way of animals passing from one to the other, the faunas tend to be unlike. And the degree of unlikeness is found to bear a rough proportion, on the one hand, to the efficiency or impassability of the barrier, and, on the other hand, to the duration of time during which the barrier has been in existence.

For example, a broad expanse of sea, particularly if there are no surface currents or prevalent winds setting across from the one coast to the other, constitutes an efficient barrier as regards the majority of land animals, and accordingly the faunas on the two sides of this expanse of sea will show distinct differences. And if there is evidence —such as great depth of the intervening sea— pointing to the barrier having existed for a prolonged period of time, then the differences are seen to be more marked.

Now it will be readily seen that what has been said agrees exactly with what we should expect if evolution be a fact. For a new type of animal coming into existence in a particular locality will gradually spread outwards from its place of origin wherever the conditions are favourable to it. If it spreads into a locality that becomes isolated, the isolated individuals will go on evolving by themselves, becoming gradually different from the parent group, the differences becoming more and more

marked according to the efficiency and the duration of the enclosing barrier.

Some of the most interesting concrete examples illustrating the relations between zoo-geography and evolution are afforded by oceanic islands, that is to say, islands which have never been connected with a continent, but have emerged from beneath the waters of the ocean through volcanic or other agency. Such islands will obviously have started their existence without any terrestrial inhabitants at all.

We will take as an example the case of the Galápagos Islands, a small group of islands, volcanic in composition, situated on the Equator 500 to 600 miles west of the South American continent. These islands are of particular interest in the history of the evolution theory, because their study played an important part in inspiring and clarifying Charles Darwin's views upon evolution.

The islands are separated from the South American continent by a 500-mile expanse of sea of over 1000 fathoms in depth, and through this deep channel there flows a constant current in a north-westerly direction which frequently deposits on their shores drift-wood, canes, fruits, and other South American products.

These rocky volcanic islands recall in their physical conditions the Cape Verde Islands, situated at a similar distance from the west coast of Africa, but, as may be expected from what has already been said, their fauna is totally different in character. While the fauna of the Cape Verde Islands is closely allied to that of Africa, the fauna of the Galápagos is closely allied to that of South America.

There are apparently no native mammals except a few rats belonging to an American genus, and a bat. There are no known amphibians. Amongst the reptiles are tortoises (from which the islands get their name, *galápago* being a Spanish equivalent of tortoise), showing distinct racial differences in the different islands and some of the individuals being of immense age as indicated by their gigantic size, about seventeen species of lizard, and eight species of snake—all of these reptiles being most closely allied to South American types. Of true land birds over forty species are known. One of these is the bobolink or rice bird (*Dolichonyx oryzivorus*), a common bird of the American continent belonging to the family of Icteridae, which in the New World takes the place of our starlings. All the other species of land birds are peculiar to the Galápagos, but apart from these islands have their nearest allies in South America.

A general inspection of the land fauna shows (1) that the animal inhabitants of the Galápagos are most nearly allied to those of South America; (2) that they are not identical with South American species, but show slight divergences in detail; (3) that species may differ as between the individual islands, but that these differences are far less marked than the differences marking off the Galápagos species from the South American.

It is clear that all this fits in exactly with what we should expect on the evolution theory, according to which immigrant species isolated on the islands would gradually evolve differences from their mainland relations, and would go on to evolve differences between themselves as at

a later period they spread to individual islands other than that which they first inhabited, the differences in this latter case being less pronounced owing to their having had shorter time in which to develop.

Before leaving the subject of zoo-geography I should allude to what is termed discontinuous distribution—the fact that certain groups of animals

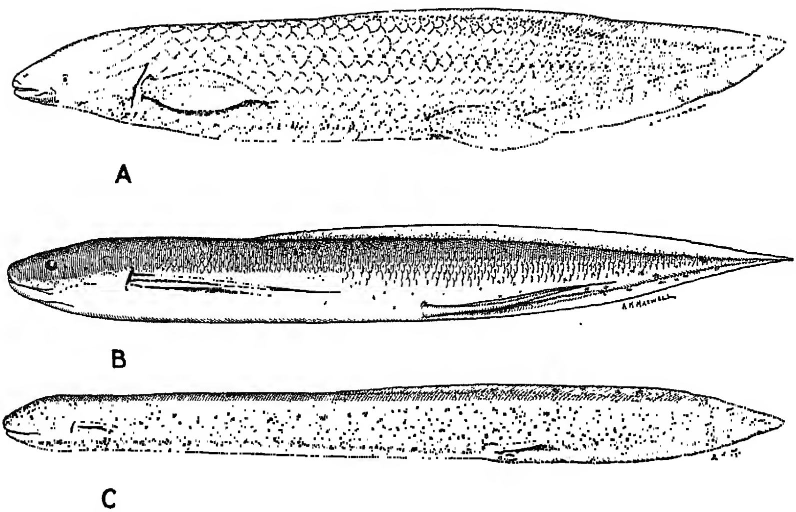



FIG. 21.—The three types of lung-fish known to exist at the present day. A, *Ceratodus* ; B, *Protopterus* ; C, *Lepidosiren*.

are represented by members resident in widely separated portions of the earth's surface while absent in intermediate regions. One of the best examples of this is the group of vertebrates known as Dipnoi or lung-fish (Fig. 21), represented by three genera, one in Tropical South America (*Lepidosiren*), one in Tropical Africa (*Protopterus*), one in Tropical Australia (*Ceratodus*). Another good example is the king crab (*Limulus*), with four

species on the coasts of Asia and one on the eastern coast of the United States of America. Another is *Peripatus*, with species in Cape Colony, Malaya, Australia, New Zealand, Chile, Guiana, West Indies.

On looking more closely into this phenomenon of discontinuous distribution it is found to be specially characteristic of animals which in structure are of an archaic type. The evolution theory gives an immediate clue to this fact, for it states that ancient types have had ample time to spread over a wide extent of the earth's surface, while there has also been ample time for changes in climate and other environmental conditions sufficient to lead to extinction except in isolated localities where the changes in conditions have not been sufficient to be fatal. In various cases of such types which possess bony skeletons palaeontology has demonstrated the truth of this belief by showing that in former geological times the distribution was continuous. Thus the lung-fishes, to-day restricted to Africa, South America, and Queensland, were practically world-wide in palaeozoic times, while the remains of lung-fish closely allied to the *Ceratodus* of to-day have been obtained from mesozoic rocks in Europe, Asia, Africa, and America.

Similarly the camel family, to-day restricted to Africa and Asia (camels) and South America (guanaco, vicuña, llama), are known as fossils from North America (Tertiary).

Again the fresh-water tortoises called Pleurodira (from the fact that the neck is bent sideways when the head is withdrawn) are to-day restricted to South America, Africa, Madagascar and the Seychelles, and Australia and New Guinea, but

are known as fossils from Europe, Egypt, India, and North America.

Finally, the group of arthropods represented to-day by the Limulus of the east coast of North America and the coasts of Malaya and neighbouring parts of Asia is represented by fossil forms practically all over the world.

In various cases of purely terrestrial animals whose distribution is interrupted by wide expanses of ocean it seems necessary to assume a pre-existent continuity of land between their present areas of distribution. For example, a group of closely allied earthworms (Acanthodrilidae) occur in South America and in New Zealand: earthworms being, it may be mentioned, a group of animals to which salt water forms an exceedingly efficient barrier. It has therefore been suggested that in former times there was a continuous land connexion between South America and New Zealand.

Such hypothetical land-bridges have played a great part in the science of zoo-geography. Personally I find it more difficult to believe in their former existence and their replacement for no apparent reason by oceans of wide expanse and great depth, than I do to believe, after the fashion of Wegener, that in the course of ages the continents undergo slow drifting movements upon the surface of the earth. Indeed I find it difficult to believe that the continental masses, composed of less dense material floating on the denser core of the earth and constantly subjected to the brake action of tidal friction, do *not* have their movement slightly retarded in relation to the denser core. But if there is any differential movement of this kind between the great land masses and the rest of the earth, what are

to-day widely separated continents such as those on the two sides of the Atlantic may well have once been in close juxtaposition and actually continuous. Such secular drifting movements of the continents would not only meet difficulties in the way of understanding the spreading of animal types across what are now great oceans, but would also meet difficulties in regard to particular land areas having been in the past subject to climatic conditions greatly different from those of to-day—as indicated, for example, by the remains of tropical flora in Greenland or the evidences of past glacial epochs in Africa.

In the preceding pages of this book I have endeavoured to indicate in outline the evidence which compels us to accept the fact of evolution. In the phenomena of embryology we are able actually to observe the process of evolution going on before our own eyes, as the zygote passes through the various steps on the way to the adult condition. This peculiarity of the living individual we are logically compelled to admit to be due, like all the other normal features of the living animal, to the influence of heredity. The individual passes through its ontogenetic evolution because of its inheriting each stage from its ancestors. And this leaves no escape from the conclusion that successive generations of these ancestors went through a gradual process of secular evolution.

On referring to the Geological Record, we found there, in spite of its imperfection and the still greater imperfection of our knowledge of it, paragraphs and chapters of the evolutionary history of animals clearly decipherable.

Turning to comparative anatomy and zoo-geography, we saw in each case varied sets of facts which in themselves appeared to be meaningless puzzles, but which are at once rendered understandable by the light of evolution. And finally, by making use of the methods devised by modern physiology for testing blood-affinity, we found that animals of differing species react to these tests in such a way as is in accordance with their being blood relations of various degrees of closeness.

Accepting, as we must, the demonstrated fact of evolution, we find ourselves confronted with the further problem which involves the cause and the method of evolutionary change. In this case the correctness of any solution at which we may arrive is no longer capable of absolute proof: all that we can do is to inquire as to possible solutions and then try to arrive at a just conclusion as to the balance of probabilities in regard to any particular one.

It is, however, clear enough what must form the foundation of any process of evolution in the animal kingdom, namely, the fact of inheritance—the fact that on the one hand the offspring resembles the parent, and on the other that this resemblance is only approximate, never exact. In accordance with the latter, the offspring, while showing the general features of the parent, always shows a slight divergence from it; in accordance with the former a means is provided whereby these little divergences can be added together in successive generations so as to produce conspicuous evolutionary changes. We accordingly pass in our next chapter to the study of inheritance.

# CHAPTER VI

## HEREDITY (INTRODUCTORY)

It is obvious that the great basic fact upon which necessarily rests the process of evolution is the fact of inheritance. It is the fact that the offspring repeats the characteristics of the parent that underlies the whole continuity and stability of animated nature; it is the fact that this repetition is never exact and complete that opens the way to a process of evolutionary change.

The study of heredity then constitutes one of the most important parts of the study of evolution. Before approaching it, it is well to note some of the difficulties in our way. One of the greatest is caused by the unreliability of much of the available evidence; there is no branch of zoology in which extreme accuracy and precision of observation, of reasoning, and of language is more needed, and there is probably none in which the absence of these has been more prevalent. It is also necessary to bear in mind how superficial and liable to mislead the features available to the observer may be. Some apparently simple dimension, for example, which to all appearance is adequately expressible by the simplest and most accurate of all methods—by a mere number—may really be, and commonly is, the end result of the workings of many and

complex factors, so that its expression as a simple number induces a totally misleading idea of simplicity.

If one observes a large number of individuals of any particular species, say man, it becomes obvious that the characteristics of the individual fall into two main classes. There are, on the one hand, characters that have been impressed upon his body during his individual lifetime—say, the loss of a limb through accident, or its abnormal size through use, or scars or other peculiarity produced by disease; and on the other hand, the much greater number of characters which are not due to anything happening during his individual lifetime.

### The Transmission of Impressed Characters

Endless debates—often induced by nothing more than the neglect to take precautions to ensure that expressions such as "acquired character" are being used in precisely the same sense by the two disputants—have taken place as to whether or not such impressed features are passed on to the descendants or not. It would greatly simplify our ideas about evolutionary progress if we could be certain that they are so transmitted. The earlier evolutionists, including Darwin himself, believed this to be the case. The great French evolutionist Lamarck made much use of such transmission as a factor in evolution. It worked according to him more especially through the use and disuse of organs. "The more frequent and sustained employment of each organ strengthens little by little this organ, develops it, increases it in size,

and gives it a power proportioned to the length of its employment; whereas the constant lack of use of the same organ insensibly weakens it, deteriorates it, progressively diminishes its powers, and ends by causing it to disappear." Thus the continued stretching out of the neck in the ancestral giraffe would cause it to become gradually lengthened: the similar stretching onwards of the body of the ancestral snake as it made its way through the vegetation would lead to its permanent elongation, while its limbs being of little use would suffer the effects of disuse and undergo gradual reduction until they at last disappeared.

It will be seen that the possibility of permanent evolutionary change being produced by such methods is dependent entirely upon the change developed in the individual, the character impressed upon his body during his lifetime, being transmitted to succeeding generations.

A moment's consideration, however, of a simple case of such impressed characters will demonstrate the extreme *a priori* improbability of their being actually transmissible to the offspring. Suppose a character to be impressed upon one of the fingers —a small injury of any kind, for example. What would be involved in the transmission of this character to the progeny? It would mean that the abnormal condition impressed upon the finger would have to influence the reproductive cells of the body in such a way as to produce in them the extraordinarily minute and yet extraordinarily potent change in their constitution that would be necessary to bring about the reappearance of the impressed peculiarity in exactly the proper position in the mass of cells constituting the body of the

new individual. In biological affairs we have to be very cautious about pronouncing anything to be impossible, but clearly the improbability of such a redevelopment of an impressed character is so great as to justify us in demanding overwhelming proof before we allow ourselves to accept its occurrence as a fact.

In spite of this improbability being so obvious the idea of the transmission of impressed characters was universally accepted until, in the "eighties" of last century, Weismann, in the course of developing his theory of the Continuity of the Germplasm, had occasion to test the foundations of the universal belief, with the result that he was able to demonstrate that the foundation of actual fact upon which it was based was hopelessly inadequate and insecure.

There is, however, even to-day a good deal of nervousness about facing the problem of evolution without the potent aid that would be furnished by the transmission of impressed characters; and, curiously to my mind, many zoologists still take seriously sporadic laboratory experiments adduced to prove such transmission. As a matter of fact we have going on around us involuntary experimentation on this subject on a scale so vast as to dwarf any experimentation on a laboratory scale into a position of relative insignificance. I allude to the phenomena of inheritance in human beings. In man we have a species of animal whose individual peculiarities—structural, functional, psychical—are familiar to us as are those of no other creature. New peculiarities are constantly being impressed upon the individual by accident, by disease, by education, and so on. Every fresh individual

that comes into the world is subjected to skilled and anxious scrutiny. Any repetition of a parental peculiarity at once excites the most lively interest.

Is there any possible escape from the conclusion that were it actually the case that impressed characters are transmitted we should have before us a mass of evidence so overwhelming as to leave not the slightest doubt in any one's mind as to the occurrence of such transmission? That there is in point of fact no such mass of evidence, but that on the contrary the recorded cases in which such transmission is asserted are very few, is a fact which to the present writer appears to constitute entirely adequate reason for adhering to the view that such transmission does not take place.

It must never be forgotten that students of evolution are apt to be strongly prejudiced in favour of accepting the transmission of impressed characters. To do so greatly facilitates their comprehension of the evolution problem. If, then, in spite of this consideration we find the great majority of capable zoologists feeling themselves debarred from doing so, that fact must count in itself as giving added weight to the opinion that such transmission does not take place.

Nevertheless, as I have already indicated, there are zoologists who stick to the idea and adduce laboratory evidence in its support. Such evidence should be regarded very critically, as it is exceedingly apt to be invalidated by neglect to guard sufficiently against disturbing factors which may be all-important. As an example of such disturbing factors I may quote particularly differences in relation to the two parents and their germ-cells that are liable to be very potent. In the first place,

the female reproductive cell is as compared with the male of relatively enormous bulk, it is in some cases millions of times the bulk of the male gamete, and consequently it provides a vehicle in which may be conveyed to the new individual substances —or for that matter living parasitic organisms— of an abnormal kind which are present in the body of the mother, and which produce by their action peculiarities in her body. Passed on to the offspring such substances will tend to produce anew in its body the same peculiarities which they induced in the parent's, and thus produce a close simulation of true inheritance.

Again, in the case of mammals—which serve as the material for much of the experimental work on inheritance—the young individual lives for a prolonged period of its development as a parasite within the body of the mother, its various processes, of nutrition and respiration and excretion and so on, being carried out by diffusion between its blood and that of the mother. Here, again, it is clear that unusual substances, or unusual proportions of substances, in the maternal blood may readily diffuse into the blood of the young individual, and produce in its body secondary results similar to those which they produced in the mother's body. And here again it is clear that experimental breeding may show what looks like true inheritance of an impressed character, whereas it is really nothing of the kind, but merely a re-development of the same feature in the new individual in reaction to the poison, or whatever it may be, passed into its system from the mother.

Such disturbing factors as have been indicated are more potent in the case of the female parent.

Consequently results invalidated by them will show a larger proportion of apparent transmissions from the mother to the offspring than from the father. Results showing this inequality should accordingly be subjected to very careful scrutiny.

Just to give an example of the better type of laboratory investigation into this subject I will quote Agar's work upon *Simocephalus*[1]—important alike for the careful and critical way in which the

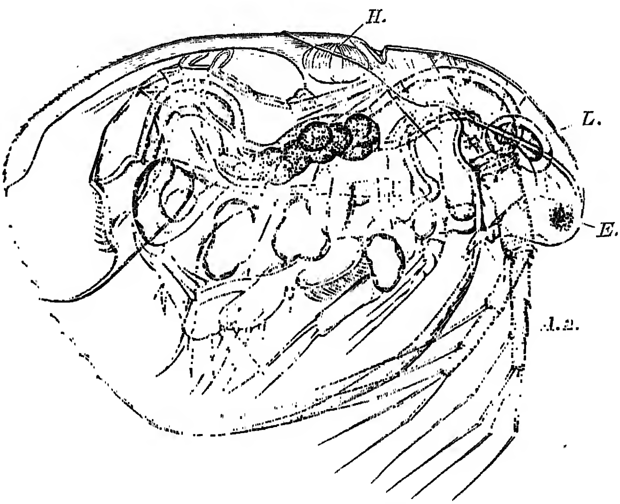



Fig. 22.—*Simocephalus*. ×30. (From Geoffrey Smith, *The Cambridge Natural History*.) A.2, second antenna; *E*, eye; *H*, heart; *L*, liver.

work was carried out, and also for the way in which it illustrates the kind of pitfalls which beset such investigations.

*Simocephalus* (Fig. 22) is a small crustacean, one of the so-called water-fleas, which are amongst the commonest inhabitants of fresh-water pools and lakes. The body is enclosed in a bivalve shell or carapace, the margins of which can be brought

[1] *Phil. Trans. Roy. Soc.*, B, vol. 205.

together ventrally so as to enclose and protect the appendages. Agar's investigation started with the observation that the rearing of young individuals in a culture of green flagellate protozoa, on which they feed, results in these individuals developing a curious abnormality, inasmuch as the lower edge of the carapace becomes reflexed outwards, so that a transverse section through the body shows the appearance illustrated in Fig. 23, B, instead of the normal shown in Fig. 23, A.

Agar took such abnormal individuals when

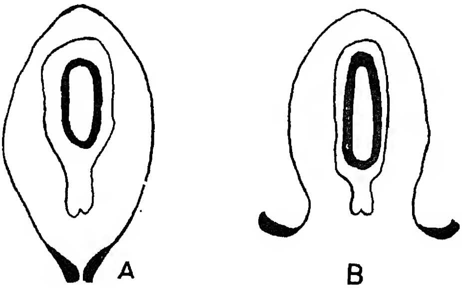



FIG. 23.—Diagrammatic transverse sections through *Simocephalus*. (After Agar.)

they had become adult, *i.e.* when they were ready to produce a batch of parthenogenetic eggs, and transferred them to ordinary water. In due course the eggs were laid, they went on with their development, and the new generation of individuals into which they developed were found to be abnormal: they repeated exactly the reflexed carapace of their abnormal parent. Here then was a definite case of a character, impressed upon the parent by an experimental change in its conditions of life, being repeated exactly by the progeny. What could be clearer as an example of the inheritance of an impressed character?

Agar, however, proceeded in proper critical spirit to check and extend his observations, and the result was very different from what might have been expected. The abnormal parents which had been transferred to ordinary water were kept there and allowed to go on reproducing, producing successive batches of eggs. It was now found that it was only the first brood that repeated the parental abnormality in full. Succeeding broods showed this less and less pronouncedly, until eventually the peculiarity had disappeared entirely, the young individuals showing no trace of repetition of the impressed character. It became clear, in fact, that it was only those eggs which had developed up to a certain point within the ovary of the parent during the period that it was subjected to the abnormal conditions that repeated the impressed character. The abnormal conditions of the flagellate culture impressed, in fact, its effect (1) upon the adult and (2) upon those eggs within the body of the adult which happened to have reached a certain stage of their development. In other words, there was here, strictly speaking, a case not of true inheritance, but simply of two generations of individuals—one still in the egg stage—on which the same set of external conditions had simultaneously impressed the same peculiar abnormality. Such a phenomenon, the impressing of a peculiarity both upon the parental body and upon the young individual in the egg stage within it, is known technically as **parallel induction.**

In the course of his work Agar made the interesting observation that occasionally a Simocephalus individual reared amongst the flagellate culture did not show in its own person the normal

reaction, but yet when removed to ordinary water and allowed to reproduce, its progeny showed the abnormality to its full extent. Such a case demonstrates particularly neatly that we have not to do with the handing on of an impressed character by the parent to its progeny, for in this case the parent has not itself developed the peculiarity.

The reader will no doubt recall to his mind in this connexion the various types of mutilation practised by man and repeated through countless generations without showing any result in the way of hereditary transmissions. Among such mutilations are circumcision, flattening of the head, filing the teeth, etc., practised amongst certain races of men, and docking the tails of various domestic animals.

I have thought it right to devote a little space to this question of the transmission of impressed characters, because it is one of great interest, human as well as purely scientific, but I do not propose to go into it in any greater detail, because to my mind the position is to-day perfectly clear that we have no justification for accepting such transmission as constituting part of the basis of evolution.

### General Features of Inheritance

It is obvious that, apart from impressed characters, the most varied individual characteristics come under the sway of heredity. The most conspicuous of these are structural. The progeny are obviously of the same kind as the parent: the

form and general appearance is clearly inherited from the parent and so also with structural individual peculiarities, stature, form of the features, monstrosities, and so on.

It is hardly less obvious that functional characteristics are similarly heritable: peculiarities of voice or of gait; personal tricks—like that of Darwin's celebrated case of the woman who inherited from her father the unfortunate habit of raising up her hand during sleep and letting it fall heavily on her nose, so that she awoke in great pain—and not merely what may be termed physical functional peculiarities, but also psychological—virtue, vice, temper, talent; all such are well known to be heritable.

Disease too—pathological developments of mind or body or function—provides frequent examples of inheritance, but here is a region of the subject in which the liability to error is extraordinarily great. In the first place, it may be not the disease itself that is inherited, but the lack of immunity against a particular pathogenic microbe. It is now well known that the supposed inheritance of pulmonary phthisis is really a case of this kind; it is merely the inadequate immunity towards infection that is transmitted, and no disease occurs in the offspring if kept from contact with the tubercle bacillus.

Again, in other cases, we have to do with the pseudo-inheritance of impressed characters alluded to on p. 81, microbic infection spreading from the parent to the egg, or embryo, as in the case of "inherited" syphilis; or with the young individual before birth being subjected to a process of slow poisoning by toxins diffusing into its blood from

that of the mother. It is clear that in none of these cases have we to do with the workings of heredity in the strict sense of the term.

Another point of general importance that must be appreciated is that hereditary characters may be present during one or more generations in latent form, giving no sign whatever of their presence. Such is the case with sexual characteristics transmitted through the opposite sex, also with the characters known as recessive (see p. 125), and with cases of reversion to characteristics visible in an ancestor two or more generations back.

It is also obviously the case that where the reproductive process is sexual the progeny may appear to repeat a particular feature of the parents in any one of three ways. Firstly, it may simply repeat the character as it existed in one of the two parents—**exclusive** inheritance. Eye colour in human beings is commonly quoted as an example of this.

Secondly, it may show **particulate** inheritance, in which the body of the offspring shows a kind of patchwork, some parts taking after the father, some after the mother. Piebald horses are an instance of this, where the light patches repeat the colour of the mother and the dark patches that of the sire. A remarkable type of case is sometimes quoted as an example of this where the two eyes are of different colours, one taking after the father, one after the mother. Such cases require very careful scrutiny, as a marked difference in colour may be due simply to one eye being in an abnormal

condition, such as having its blood-vessel much dilated through disease, accident, or operative interferences.

Thirdly, the offspring may show **blended** inheritance, the particular feature showing a complete blending of the paternal and maternal conditions. Stature and colour in man afford good examples of blended inheritance. It is obvious that there is no sharp line of demarcation between particulate and blended inheritance; particulate inheritance on a smaller and smaller scale would pass by insensible gradations into blended inheritance.

Lastly, we should note that the power of the two parents of influencing a particular feature in the offspring may differ greatly; one may be distinctly **prepotent** over the other.

## Variation

I have already alluded to the fact that the offspring never repeats exactly the characteristics of the parent. It invariably fails to attain identity in its characteristics with its parents, and the extent of its failure to do so, differing in different individuals, is what we term variation. Variation I regard as an expression of the inherent instability characteristic of all living matter. In a complex animal, whose whole being is a complicated bundle of adaptations, each organ minutely adjusted to work with the other organs, and the organism as a whole intimately adjusted to its environment, large departures from the normal are liable to be physiologically impossible, *i.e.* to be incompatible

with continued life, and they are correspondingly rare.

Small variations, on the other hand, are omnipresent. It is only necessary to examine carefully a few hundred specimens of some animal of moderate complexity to see how the individuals all differ slightly—in size, in proportion of their parts, in shape, in colour. Every feature shows a small departure from the mean. Without in fact making special investigations we are all of us aware of this fact from our observations of human beings. The old saying has it that men are born equal, but we all know from our own experience that this is untrue. Even the sons of one family—with the same parents and the same set of ancestors right back—invariably show inequalities in appearance and structure and aptitudes and weaknesses.

If we proceed to the more detailed investigation of the phenomena of heredity, it is clear that we may use either of two different methods—the statistical method and the experimental. In the first method we use the methods of statistical science, examining the phenomena in large numbers of cases and extracting from this mass observation the logical conclusions. As the methods of statistics are mathematical methods it is necessary in such investigations to confine oneself to the study of characteristics which can be expressed precisely by numbers—such as, for example, some particular dimension, or the number of joints in some segmented structure, such as the body of a worm or the feeler of a lobster.

In the experimental or intensive method, on the other hand, we start from a particular pair of parents and follow their descendants from genera-

tion to generation, observing to what extent some particular feature is transmitted throughout the chains of descendants. It is obvious that this method will be most suitably carried out by the experimental breeding of some small animal which reproduces comparatively rapidly.

Before proceeding to consider these two methods of observation and the results that have been obtained by their use it will be of advantage to consider shortly the mechanism by which inheritance takes place.

# CHAPTER VII

## THE CYTOLOGICAL BASIS OF INHERITANCE

THE individual begins his existence as a simple cell—the zygote or fertilized egg, formed by the fusion together of two reproductive cells or gametes, derived one from each of the parents. This applies to the overwhelming majority of animals. It applies alike to the lowly worm and to the mammal or bird. In the vast majority of cases the zygote shows none of the obvious features that characterize the adult. For example, it is impossible to recognize in the zygotes of three very different types of pelagic fish any of the differences that make the adults distinguishable from one another at a glance. Each one of them is a simple cell composed of cytoplasm and nucleus, and if the three zygotes are distinguishable by the expert it is through their possessing peculiarities—for example, in size or colour—which are of quite a different nature from their peculiarities in the adult phase of their life. And yet each one of these zygotes contains, although in invisible form, these peculiarities which characterize the parent species. This is demonstrated by keeping the three zygotes alive and healthy *under identical conditions*, so as to eliminate the possibility of any moulding influence on the

part of the environment, when each one will be seen to unfold gradually its specific peculiarities and become recognizable as an ordinary adult of its particular species.

It might be argued that this does not necessarily hold for all creatures. A man in the zygote stage may be a primitive savage, an imbecile, a Napoleon, a Shakespeare, a Newton, a Darwin—it is impossible to say, but it might be argued that as he passes through the succeeding stages of development within the maternal body his personality becomes moulded in some way by its influence. There is no evidence to support this idea. On the contrary, it seems clear that the zygote even within the uterus of a healthy and normal mother is entirely unaffected by her personality. This can be demonstrated by experiment. If at an early stage of its development the egg of a particular breed of animal (*e.g.* a rabbit or a guinea-pig) is extracted from the uterus of its mother and inserted by appropriate surgical methods into the uterus of a healthy mature female belonging to a different breed of the same species it will, in successful cases, proceed to complete its development within the body of its foster parent. In such a case it is found that, when brought forth, the young animal is obviously of the breed of its original parent, and shows no trace whatever of having been modified by the body of the different type of individual in whose uterus it has gone through by far the greater part of its developmental history.

We may take it then that the specific peculiarities of the adult parents are already present, though invisible, in the zygote. How did they get there? It is obvious that they must have been contained

in the two gametes which by their fusion constitute the zygote. Further, they must have been contributed approximately equally by the two gametes, seeing that on the average the characteristics of the individual are inherited equally from the two parents. The two gametes, however, although they carry equal loads of heritable characters are commonly very different in size (Fig. 1, p. 12); the maternal gamete or egg may be many millions of times the bulk of the paternal gamete or spermatozoon. This clearly implies that it is not the substance of the gamete as a whole which acts as the vehicle of heredity; it must be some part of the gamete which is approximately equal in quantity in the two types of gamete.

This consideration clears the way to approach the problem: What is the actual material basis or vehicle of heredity? It indicates that we must make a minute study of the two types of gamete with the object of determining whether, in spite of their discrepancy in size, there is any corresponding element in both of them approximately equal in amount; for if we succeed in finding such a component we shall probably have succeeded in locating the vehicle of heredity.

It will be recalled that the zygote is a single cell, a usually spherical mass of living substance or protoplasm. One of the characteristics of the typical cell is that the government of its living activities is centralized in a special modified portion of the protoplasm called the nucleus. A large proportion of the nucleus is made up of a special dense deeply-staining substance, **chromatin**. That this is, or contains, the all-important part of the nucleus is indicated by the fact of its constancy,

other parts of the nucleus fading away and being replaced from time to time.

As the living activities of the individual cell are controlled by the nucleus, and as the complex animal individual is composed of myriads of cell individuals, we are justified in suspecting that the living activities of the whole individual, including its repetition of parental features, are also controlled by the nuclear material of the body. As the chromatin is the chief part of the nucleus we are further justified in concentrating our attention specially on it when hunting for the material vehicle of heredity.

When we examine the two types of gamete we find that each contains chromatin, but at first sight this seems to be very different in amount in the two cases. For example, in Fig. 1 (p. 12) the amount of chromatin in egg and spermatozoon looks quite different. This appearance, however, is deceptive, the chromatin of the spermatozoon being temporarily condensed into as small bulk as possible, in correlation with the minute size and active movements of the spermatozoon. When the process of fertilization or syngamy is studied microscopically it is found that the chromatin of the spermatozoon after entering the egg gradually swells up, and when it has reached the stage of being no longer any denser than that of the egg it is seen to be identical in appearance with it; the egg now contains two nuclei, one the original maternal or egg-nucleus, and the other the immigrant paternal or sperm nucleus, with identical amounts of chromatin—it being in fact quite impossible to tell which is which (Fig. 24, C and D).

We see then that the chromatin possesses the

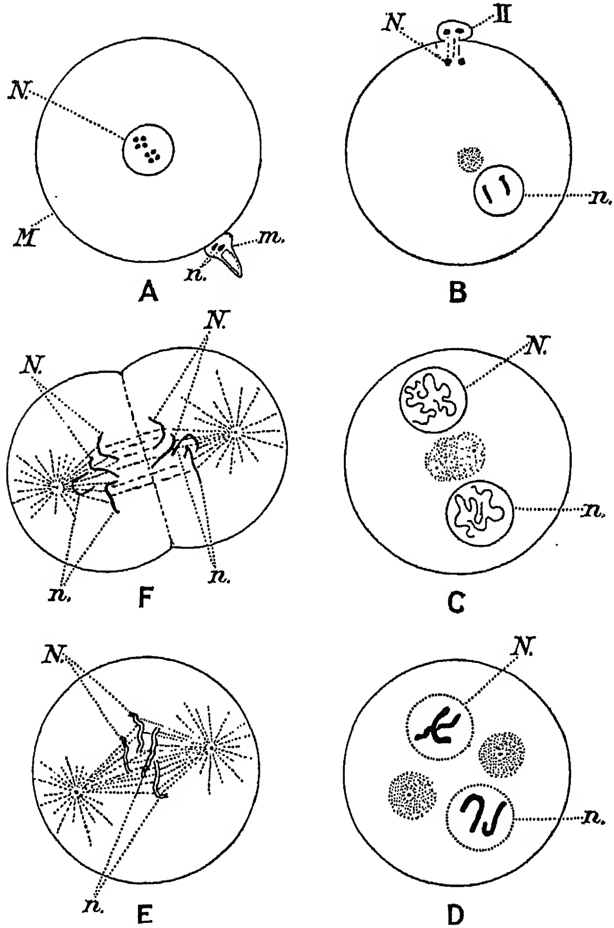



FIG. 24.—Syngamy in *Ascaris*. (From Graham Kerr, *Zoology for Medical Students*.) A, The pear-shaped spermatozoon or microgamete is seen attached to the side of the spherical egg or macrogamete; B, the sperm-nucleus is now within the substance of the egg, part of the egg-nucleus is being got rid of at the upper boundary of the egg; C and D, the egg-nucleus and the sperm-nucleus have now become indistinguishable in appearance, each contains two chromosomes (haploid number); E and F, mitosis is taking place, each of the four chromosomes splitting longitudinally into two, so that each daughter cell will contain four chromosomes, the normal or diploid number. *M*, macrogamete; *m*, microgamete; *N*, nucleus of macrogamete; *n*, nucleus of microgamete; II., part of egg being separated off ("second polar body").

quantitative and other characters which we should demand of the substance which represents heredity, and as no other substance is known to do so we are justified in adopting the working hypothesis that chromatin is actually the physical vehicle of heredity.

That this working hypothesis is in fact a true theory appears to be demonstrated by the behaviour of the chromatin in stages subsequent to the zygote. A characteristic feature of heredity is the way that it dominates the whole individual. There is no fragment of the complex body that is not under its sway. It follows then that, as the zygote resolves itself, by a process of fission repeated over and over again, into the community of innumerable cell-individuals that constitute the body of the adult, the heredity substance, whatever it is, must undergo a process of equal partition amongst all the various individual cells. Now this is precisely what the chromatin does.

When the cell, whether the zygote or one of its descendants, is about to divide into two it becomes apparent that the chromatin of its nucleus consists of definite pieces named **chromosomes** (Fig. 24, D), and it is a remarkable fact that in each ordinary cell of a particular species of animal these are of the same number.[1] As the unicellular stage, the zygote, already possesses this same number of chromosomes, it follows that each of the two gametes, which by their fusion form the zygote, must contain only half the normal number. Thus in the round-worm *Ascaris*, illustrated by Fig. 24, the ordinary chromosome number (called technically the **diploid** number) is four, while the gamete number (called technically the **haploid** number) is two.

[1] Apart from the qualification mentioned on p. 104.

It is, further, a very general and highly characteristic feature of the successive cell-divisions that, with the onset of the process of division, each chromosome becomes split longitudinally with the greatest accuracy into two daughter chromosomes (Fig. 24, E), which presently move apart and pass one to each of the daughter cells (Fig. 24, F). It is obvious that this very generally occurring type of nuclear division, known technically as mitosis or karyokinesis, repeated over and over again as the unicellular zygote becomes the multicellular adult, brings about just such an equal partition of the chromatin, as has been postulated, amongst the cells constituting the adult body.

As has already been seen the chromatin of the zygote stage has been derived in equal amounts from the male and female parents. In the case of the worm illustrated in Fig. 24 two chromosomes were paternal and two maternal. But the process of mitosis ensures that this condition is passed on to the daughter cells, and to their descendants in turn, the result being that each cell in the completely developed body has its activity governed by chromatin half of which is paternal in origin and half maternal.

In view of the phenomena described, the general occurrence of which has been confirmed by observations on an immense variety of animals, it is, in my opinion, no longer justifiable to harbour any doubt that the chromatin is the vehicle of heredity.

But we are justified in going a great deal farther than merely to take up the position indicated. The accurate longitudinal splitting of the chromosomes has been alluded to. In relation to this process the chromosomes very generally take on an

elongated more or less rod-like form, in many cases becoming drawn out into a long slender thread, just before the process of splitting takes place. This can only mean that there takes place a halving not merely of the entire mass of the chromosome, but also of each little bit of chromatin along the whole extent of its length. And this in turn can only mean that the substance of the chromosome is not homogeneous but is differentiated along its length—the longitudinal splitting ensuring that each one of the differing bits of chromosome is precisely halved between the two daughter chromo-

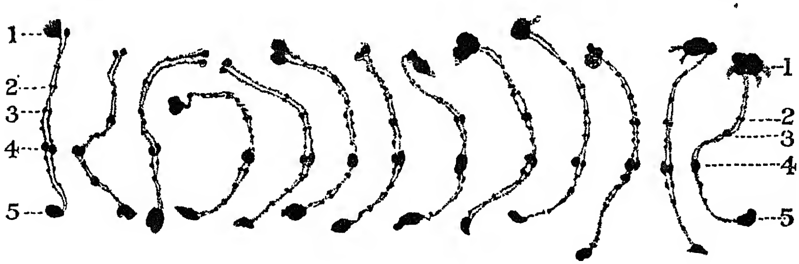



FIG. 25.—Corresponding chromosome drawn from thirteen different specimens of a locust, *Phrynotettix*. (From Agar, *Cytology*.)

somes. As a matter of fact it is sometimes possible even by observation of the superficial appearance of the chromosome to see that such differentiation along its length actually exists, little swellings being in some cases clearly observable at corresponding positions along the length of the chromosome in different nuclei (Fig. 25).

Regarding the chromosome as the vehicle of heredity, this longitudinal differentiation of the chromosome would mean that different components of the heritage are represented by different bits of the chromatin (gens), or in other words, that the material representatives of the various hereditary

features are arranged in linear fashion along the length of the chromosome. That this is a necessary implication of the longitudinal splitting of the chromosome, recognized by Flemming in 1879, has long been grasped, but its truth has been driven home of recent years by the wonderful studies of the facts of inheritance carried out in America by Morgan and his pupils. Not only have these studies provided what is practically a demonstration of the fact that the bits of hereditary substance representing the various heritable features are arranged in linear fashion along the length of the chromosome, but they have even rendered possible the attempt to map out roughly the location of the various gens along the length of the chromosome.

As already indicated it is an essential feature of syngamy or fertilization that the two uniting gametes shall each have the normal or diploid chromosome number reduced to the half or haploid number, so that their fusion will merely restore this number to the normal. Some of the most fascinating modern work has to do with this phenomenon of **meiosis** or halving the number of chromosomes during the preparation of the gametes. It has now been demonstrated in a large number of cases that the halving is brought about by the original chromosomes adhering together in pairs. This is the process known as **syndesis**.

The chromosomes of the ordinary cells of the body are of an even number, equal numbers having been contributed by the two parents. Now the individual chromosomes may sometimes be observed, when carefully examined with the highest powers of the microscope, to possess special peculiarities of form by which the expert cytologist is able to

recognize them individually. He may give them names, say *a*, *b*, *c*, and so on. In each cell of the body he finds a corresponding set of chromosomes, or rather two corresponding sets of chromosomes, for there are two *a*'s, two *b*'s, two *c*'s, and so on, one set paternal in its origin, the other set maternal. The two corresponding chromosomes, say the two *a*'s or the two *b*'s, are called by the specialist **homologous** chromosomes.

Now when syndesis takes place by the chromosomes approaching and adhering together in pairs it is always two homologous chromosomes that so unite. In many cases where they come together side by side it can be observed further that the two chromosomes are arranged with corresponding ends in the same direction: they are never arranged "heads and tails". These phenomena teach an important lesson: they would appear to indicate clearly the existence of an attractive force between homologous chromosomes; but the fact that the two syndetic chromosomes are similarly orientated leads to the further important conclusion that homologous *parts* of the chromosomes attract one another.

If, however, it be the case that there is an attraction between like or homologous portions of chromatin, and if the chromatin be the vehicle of inheritance, then it would further follow that the portions of chromatin representing the various heritable qualities would tend to concentrate together according to their degree of likeness, so that each particular heritable feature would have the chromatin representing it closely clumped together. The special interest of this is that the concentration together of the chromatin representing the various

heritable features, each by itself, would lead to results which would closely simulate what would occur were the various heritable features represented by distinct independent *units* of hereditary substance. Such clumps of hereditary substance, each representing a particular hereditary feature, are the "gens" already mentioned. It will be well to guard ourselves against falling into the widespread error of regarding these gens as necessarily isolated material particles: they may be, and in my opinion are more likely to be, simply locally differentiated portions in a continuous substance.

The pairing of the chromosomes is a prelude to the cell containing them undergoing fission into two, and a little later this process is repeated so that each of the cells in which the pairing took place is now represented by a brood of four cells, each potentially a young gamete. An apparent splitting of the chromosomes takes place in relation to each of the two divisions, but one of these is merely the separation of the two homologous chromosomes which had temporarily adhered together in the process of syndesis, the other is a true splitting process like that in ordinary mitosis.

In order to get a clear idea of these phenomena it is advisable to express them in the form of a simple diagram (Fig. 26). To reduce the matter to its greatest simplicity only a single pair of homologous chromosomes is represented, and each is supposed to carry only a very small number of hereditary characters, represented by the first three letters of the alphabet.

In the left-hand column (PS) syndesis has not yet taken place; the two homologous chromosomes,

one paternal (*a b c* ) and one maternal (*A B C*), lie separate. In S syndesis has taken place, the two chromosomes adhering together side by side, with like poles pointing in the same direction. When mitosis takes place this temporary union is dissolved, one daughter cell receiving an *A B C* chromosome and the other an *a b c* chromosome. A second division takes place, each chromosome now splitting in the normal fashion, so that there

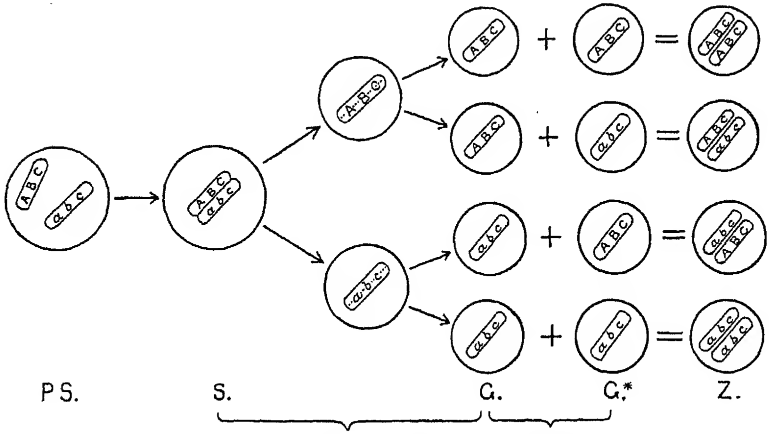



FIG. 26.—Diagram to illustrate syndesis and syngamy. Each circle represents a cell-nucleus and in each is represented a single chromosome, or two homologous chromosomes, supposed to carry three hereditary characters represented by the first three letters of the alphabet. PS, nucleus before syndesis has taken place ; S, syndesis ; G, gametes ; G*, gametes from another individual ; Z, zygotes.

arise two cells in which the chromosome is *A B C* and two in which it is *a b c*. In other words, each syndetic cell has given rise to a brood of four descendants (Fig. 26, G), of which half are *A B C* and half are *a b c*. These four cells are young gametes, and it follows that of all the gametes produced half contain the chromosome in the *A B C* form and half in the *a b c* form.

The function of the gametes is to undergo syngamy and so bring into existence the new zygote individual. The column marked G* shows the four corresponding gametes from another individual, with which the first set undergo syngamy. It is obvious that each *A B C* gamete in column G may undergo syngamy either with another *A B C* gamete or with an *a b c* gamete. Similarly, each *a b c* gamete in column G may undergo syngamy with an *A B C* gamete or with another *a b c* gamete. Assuming there is no disturbing factor at work these four types of syngamy will occur with equal frequency, the result being that out of, say, a thousand zygotes (Fig. 26, column Z) 250 will be pure *A B C*, 250 pure *a b c*, and two lots of 250 will be mixed *A B C* and *a b c*.

Suppose we substitute for the capital and small letters of the diagram some definite hereditary character occurring in different form in the two parents—say blackness and whiteness in a particular breed of fowl—we should obtain 250 new individuals that are pure black, 250 that are pure white, and 500 that are mixed black and white. As this is precisely the kind of result that experimental breeding gives us we may take the latter as a final proof of the fact that chromatin is the vehicle of heredity.[1]

## Sex Chromosomes

One of the most interesting zoological advances of recent years has been the linking up of the

[1] As is the case with so many of the more important advances made in recent years regarding the relations between the phenomena of inheritance and the cytological phenomena of the germ cells, we owe the correlation of the facts of Mendelian inheritance with the facts of meiosis to an American investigator. It was Sutton who I believe first, in 1902, brought out this correlation.

determination of sex with peculiarities of the chromatin of the gametes. It turns out that one or other of the two sets of gametes—most usually the male, but apparently in some cases the female—exist in approximately equal numbers in two different types which we may call (A) male-producing and (B) female-producing, and the sex of the new individual depends normally upon which of these two types happened to be concerned in the formation of the particular zygote. The sex-determining gametes of the two types being approximately equal in number, the number of resultant individuals is also divided approximately equally between the two sexes.

The two types of sex-determining gamete are distinguished from one another by chromosome differences varying in detail somewhat in different cases. The simplest type of case, already known to exist in a large number of different animals, is illustrated by Fig. 27, in which for the sake of simplicity, as in the preceding figure, only a single pair of homologous chromosomes is shown where syndesis is taking place (S). In addition to the ordinary chromosomes there is seen to be a small body indicated by X. This is in its nature really a small extra chromosome, and for reasons that will become apparent presently is known as the **sex chromosome.**

I have already described how the ordinary chromosomes of column S in the figure become divided up between the group of four gametes (G) by two successive mitotic divisions, but we have now to trace out the behaviour of the sex chromosome. This is found to show two different variations, namely, that in one or other of the two

mitotic divisions the sex chromosome does not split into two but passes over bodily into one of the daughter cells. In the upper half of the diagram this is the case in the first mitotic division, in the

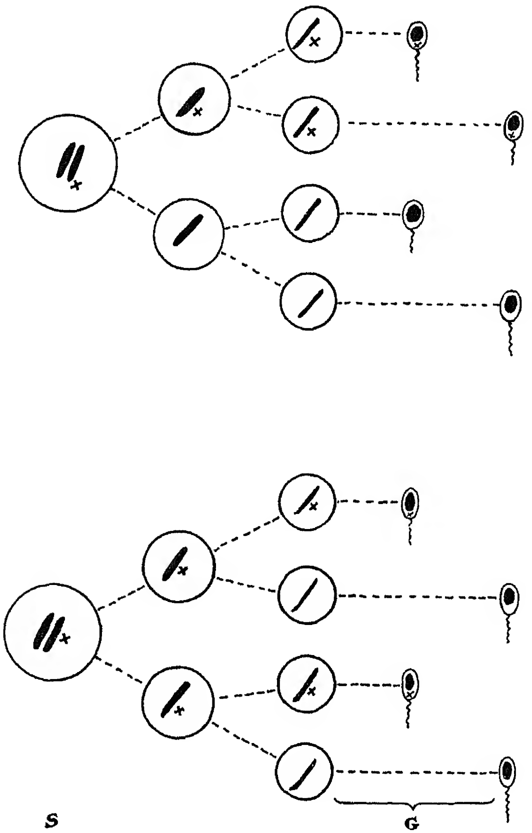



FIG. 27.—Diagram to illustrate sex-determining spermatozoa. Those that contain the X-chromosome will produce female individuals.

lower half in the second. But it will be seen that the end result is the same in the two cases, namely, that out of the brood of four resulting spermatozoa two contain a sex chromosome and two do not. Or if we speak not in terms of the brood of four

but of the myriads of spermatozoa produced by the individual half contain the sex chromosome and half do not.

Whereas in such a case the spermatozoa are divided into two sets, differing in the presence or absence of a sex chromosome, the eggs, on the other hand, are all alike in their chromosome contents; every one contains a sex chromosome. Consequently when syngamy or fertilization takes place the resultant zygote will contain two sex chromosomes or only one, according to whether or not a sex chromosome has been brought in by the fertilizing spermatozoon.

Zygotes with two sex chromosomes are female; they grow up into female individuals, every cell of which contains two sex chromosomes. Zygotes with only one sex chromosome are male; they grow up into male individuals, each of whose cells contains only a single sex chromosome.

Phenomena similar to those described have now been observed in quite a number of different animals. There are differences in detail. Sometimes it is apparently the eggs rather than the spermatozoa that are divided into two sets. Sometimes the "X-" chromosome of the one lot of gametes may be represented by a "Y"-chromosome in the other lot. Sometimes the sex chromosome is large, sometimes it is small, sometimes it is free, sometimes adherent to one of the ordinary chromosomes. But ignoring such differences in detail we may take it as well established as a general principle that the determination of sex is due to one or other set of gametes being divided into two categories—male-producing and female-producing—and that these are labelled, so to

speak, by observable differences in their nuclear structure.

## Gonad and Soma

Modern biology draws a sharp distinction between the cells of the body in general, specialized for the various functions of ordinary life, and the reproductive cells, without specialization for the ordinary bodily functions, but possessing the power of giving rise—usually in response to the act of syngamy—to a new individual. The first category of cells constitute the **soma**, the second category the **gonad.**

The individual in its earliest—zygote—stage consists of course entirely of gonad; it has been formed by the fusion of two bits of gonad from the two parents. As in the process of development it assumes the multicellular condition specialization gradually becomes apparent in those cells which constitute the soma. One of the interesting results of modern research is the discovery in a few cases that the somatic portion of the cell-community becomes definitely labelled as such at an exceedingly early stage. The best example of this is the parasitic round-worm *Ascaris*. In Fig. 24, F (p. 95), the zygote of this animal was shown in process of dividing into two cells. Each of these in turn undergoes fission, but a difference in detail is seen in the way in which the two cells behave. One of them divides in the normal fashion, each of its chromosomes splitting longitudinally, as in Fig. 24, E. In the other cell there takes place a peculiar process, in which the end portions of the chromosomes are cast off and

simply used as food material by the protoplasm, with the result that the two daughter cells possess nuclei in which the amount of chromatin has been diminished below the normal.

As development proceeds this process of eliminating chromatin by certain cells is repeated several times, and eventually a condition is reached in which the new individual consists of a vast community of cells containing the diminished amount of chromatin with a little patch of cells in which the chromatin has not been diminished. The latter patch of cells constitutes the gonad, all the remaining cells the soma.

The importance of these phenomena lies not in the details of what happens—in fact these details are not yet by any means thoroughly understood—but in the fact that their occurrence provides a kind of label by which somatic cells can be distinguished from the cells of the gonad. The fact that this label is available makes it possible for us to grasp the fact, so far as *Ascaris* is concerned, that the soma becomes differentiated off from the gonad at an extraordinarily early period in the development of the individual. If this is a general rule—and I cannot help suspecting that it is in spite of the fact that in very few cases has it been possible so far to detect characteristics which distinguish the two types of cell in the clear way that occurs in *Ascaris*—then we see that it is in complete accordance with what was said in Chapter VI. regarding the non-transmission of features impressed upon the soma of an animal after it has become differentiated from the gonad.

It is also apparent that such phenomena suggest

to the evolutionist fascinating vistas into the past and future history of living things. Looking back through the past ancestry of the living individual we perceive a continuous strand of gonad substance stretching without a break through the whole period of evolutionary time, back into the infinitely remote past, back to the very first substance that began to "live". In each successive individual of the ancestral chain we see something not new in itself, but merely a little bit of this continuous strand which becomes conspicuous by its active growth and the specialization of its parts.

Or, putting the matter somewhat differently, as is expressed in Fig. 28, we see continuous through the bodies of the individuals that form the chain of descendants an immortal line of living substance, the body of the individual being a portion which is shunted off into the siding which comes to an end in death.

We have accordingly to modify entirely our ordinary conception of parent and offspring, for we see that the parent does not actually produce its reproductive cells; it is rather a kind of foster

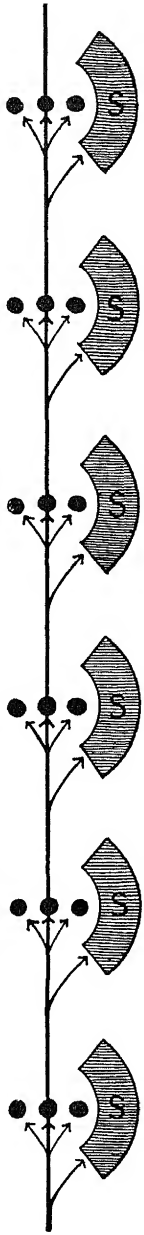



Fig. 28.—Diagram to illustrate the continuous strand of gonad associated with an ancestral chain of individuals. The bodies of the successive individuals (S) are shown as side-tracked off the line of gonad. The three circular masses of gonad corresponding to each individual body represent the portions which become functional gametes, the living substance of any one of which may fulfil its destiny and have its existence continued onward in the next generation.

parent which shelters, transports, and nourishes the bit of gonad which it has inherited and which will in turn bud off the bodies of future generations.

## BOOK FOR FURTHER STUDY

1919. Morgan. *The Physical Basis of Heredity.*

# CHAPTER VIII

## THE STATISTICAL STUDY OF INHERITANCE

STATISTICS being a branch of the science of numbers the statistical method of inquiry is appropriate only for the investigation of hereditary characteristics that are capable of exact numerical expression.

Such a characteristic is stature, and we may make use of it to provide a simple example of statistical inquiry—Galton's and Pearson's investigations of the extent to which stature is influenced in man by the stature of the parents.

Fig. 29 illustrates the result of such inquiry into the relation of the stature of sons to that of their fathers, plotted out in the form of a graph. The figures along the base-line (abscissae) represent in inches the statures of the fathers, while the figures along the left-hand side of the diagram (ordinates) represent the mean stature of the sons of each father. After determining the mean stature of each family of sons a dot is placed on the same horizontal level as this particular figure (ordinate), and on the vertical line corresponding to the stature of the father. By repeating this observation on a great many families of sons, plotting the results down on squared paper and then joining all the dots into a continuous line, a curve is obtained which embodies the general result, and is capable of further study.

It is obvious that this line must fall between two limits. It is conceivable on the one hand that the mean stature of the sons might simply be the same as that of the father. In this case a family of sons belonging to a father 64 inches in height

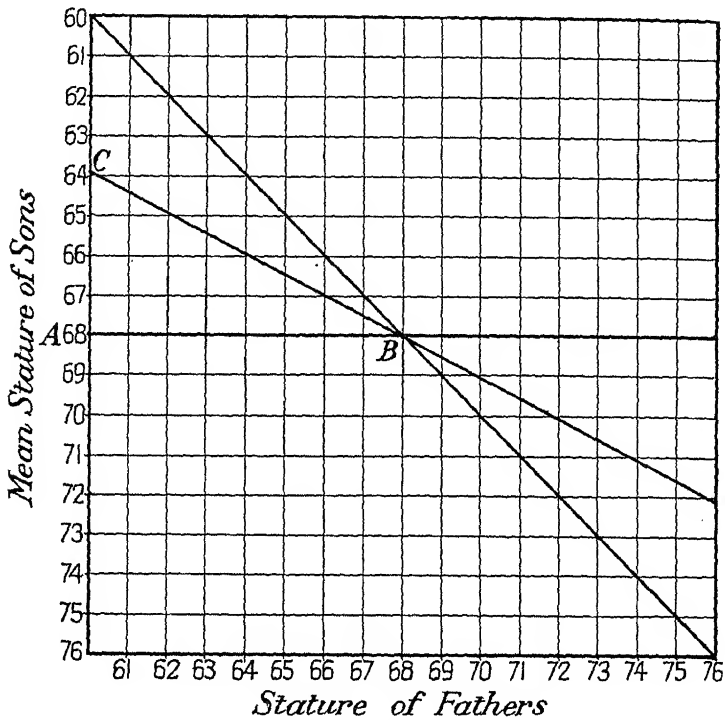



FIG. 29.—Graph illustrating the relation of the stature of sons to that of their fathers. Constructed from observations made by Pearson.

would have a mean height of 64 inches, those belonging to a father of 72 inches would have a mean height of 72 inches, and so on. The whole series of observations joined into a continuous line would be a diagonal.

On the other hand, it is conceivable that the stature of the sons would be absolutely uninfluenced

by the stature of their fathers; their mean stature would simply be that of adult males of the race. The dots representing the various observations would in this case all be situated at the level of the ordinate representing the mean stature of the adult males of the race—68 inches in the case illustrated in Fig. 29; in other words, the line formed by them would be the horizontal line at this level.

The horizontal line A B and the diagonal line inclined to it at an angle of 45° represent, then, in the figure, the possible limits. The line formed by the actual observations (C B) might theoretically lie anywhere between these two limits. Were there no correlation between the stature of the sons and that of the fathers the line would be horizontal; with higher and higher degrees of correlation it would be inclined to the horizontal at greater and greater angles until, in the case of complete correlation, the angle would be 45°. The degree of correlation varying with the slope of the observation curve, a convenient way of expressing it is by giving the tangent of the angle A B C—varying from 0 when the line is horizontal, up to 1 or unity when it is at 45° to the horizontal. This number is termed the **coefficient of correlation.**

The curve shown in Fig. 29 (C B) was obtained by comparing the feature studied (stature in this case) with the corresponding feature in one of the two parents, but in many such studies use is made of what Galton called the "mid-parent", *i.e.* the mean of the two parents in regard to the particular feature under investigation.

Investigations of the kind indicated, carried out in regard to various different features, show it to be a general principle that, as in the case shown,

the coefficient of correlation is less than unity, in other words, the mean character of the offspring tends not to repeat exactly or to exaggerate the character of the parent but to swing back towards the mean of the race. Here we have brought out one of the conspicuous results of the statistical study of inheritance—that there exists a tendency to regression towards the mean of the race. The practical importance of this conclusion, if sound, is obvious: it means that on the whole the progeny tends to be more commonplace than the parents. When a parent is outstanding in any way—in goodness or badness, in intellectual or artistic power, in stature, or in any other character—there is always this tendency for the descendants to be dragged back towards the mean of the race.

From the purely scientific point of view the principle of regression is of interest from its emphasizing that the heritage of the individual is concerned not merely with the immediate parents but with the race in general as represented by the large number of more remote ancestors.

In Galton's day it was natural to regard each of these more remote ancestors from the point of view of their individual contribution towards the total heritage of the individual, and Galton endeavoured to arrive at a precise idea of the proportional amount of the total heritage contributed by each grade of more and more remote ancestors. The conclusions at which Galton arrived were based on the consideration of a large mass of data regarding inheritance first in human families and later especially in the case of Basset Hounds —a type of dwarf blood-hound bred on a large scale by Sir E. Millais, who started his kennel

in the 'seventies with ninety-three imported individuals. Careful pedigree records were kept, dealing with coat-colour and other features, and Galton, tracing back the ancestral history of various individual hounds through these records, was able eventually to form an idea as to the contribution made to the complete heritage of the individual by its various ancestors. As a result he was able to formulate his "Law of Ancestral Inheritance", according to which the total heritage expressed as unity is the sum of the following series—

$$[\cdot 5 + \cdot 5^2 + \cdot 5^3 + \cdot 5^4 \;.\;.\;.\;]:$$

the parents together contributing $\cdot 5$ of the total heritage, the grandparents together $\cdot 5^2$, the great-grandparents $\cdot 5^3$, and so on—the ancestors of any particular generation contributing together a fraction of the total heritage equal to $\cdot 5$ to the power expressed by the number of generations back.

The contribution of the *individual* ancestor would obviously be, according to this law, one-quarter ($\cdot 5^2$) in the case of the parents, one-sixteenth ($\cdot 5^4$) in the case of the grandparents, one-sixty-fourth ($\cdot 5^6$) in the case of the great-grandparents, and in the case of an ancestor of the $n$th degree $\cdot 5^{2n}$.

Subsequent workers along similar lines have modified these figures, thus Pearson reduces the proportional contribution of the more remote ancestors.

It is necessary in a book like this to mention the "Law of Inheritance", as the student of heredity is sure to come across references to it. Apart from its importance in the historical development of the science of heredity its main interest would appear to lie in the way it again emphasizes the fact

that the individual of to-day is closely tethered to the past of the race.

Some of the most interesting results of the statistical method deal with the failure of the individual to show complete inheritance, *i.e.* with what is usually called variation. For example, we can profitably use this method to inquire into the degree of variability of some characteristic of an animal that can be expressed numerically—such as

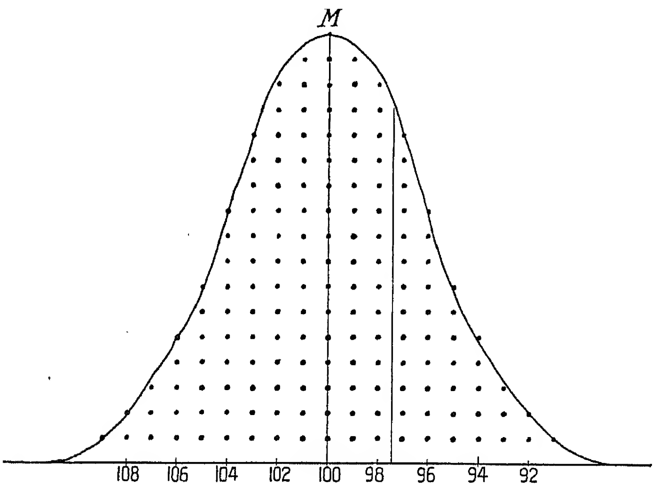



FIG. 30.—Polygon of variation.

a particular dimension, or the number of joints in a segmented body. The results so obtained may be expressed in a graph, as in Fig. 30, which represents a series of imaginary observations of some imaginary character in a wholly imaginary animal, but which gives an accurate idea of the kind of results obtained by actual observation. The particular character is supposed to vary round about 100. The scale of numbers or dimensions is arranged along the base-line, and each observation

as it is made is plotted down vertically over the particular number on the base-line. When a large number of such observations are plotted down on squared paper they commonly form a figure of the type shown—the so-called polygon of variation.

This figure is of mathematical interest inasmuch as its boundary forms a curve of the type known to mathematicians as the normal curve of error. A skilled marksman firing on a windless day at a vertical line on a target would group his shots in the neighbourhood of the vertical line, and the distances of the individual shots from this vertical line when plotted as a graph would form such a curve of error. Or again, the same type of curve would be obtained by plotting out the amount of error of a large number of clocks.

It is obvious that such a curve at the first glance affords us information regarding the degree of variability of the particular character we are investigating. It is clear that if the degree of variability be small the observations will be crowded close to a vertical and the curve will be tall and narrow; on the other hand, if the degree of variability is high the observed deviations will extend far out and the curve will be low and its spread great.

The degree of variability ascertained from such a curve may be conveniently expressed numerically. One of the simplest methods of doing so is to give the "**Probable Error**". A vertical line is drawn bisecting the area of the polygon, or in other words, having the same number of observations on each side of it; this line is termed the **median**.[1] If now

[1] Not to be confused with this term is the term "**mode**". The mode is a vertical line drawn through the most frequently occurring dimension. In Fig. 30 median and mode are coincident, but in a skew or lop-sided curve they are not so.

the half polygon, bounded on one side by the median, is in turn bisected by a vertical line, the distance of this line from the median is the "probable error", and expresses the degree of variability on that particular side of the median. In Fig. 30 the probable error towards either side is obviously a little over $2\frac{1}{2}$.

There are of course other ways of expressing the same thing—such as, for example, measuring the deviation of each particular case from the mean and taking the average of the lot. To be preferred to this average deviation is what is termed the **standard deviation** expressed usually by the letter $\sigma$.

$$\sigma = \sqrt{\frac{\Sigma(d^2)}{n}},$$

*i.e.* the individual deviations ($d$) are squared, the squares added together and divided by the number of cases ($n$), and finally the square root extracted from the number so obtained. Another way of stating this result is to express it as a percentage of the mean, in which case it is termed the **coefficient of variation** and expressed by the letter V.

$$V = \frac{\sigma \times 100}{\text{mean}}.$$

Probable error, average deviation, and standard deviation are not identical; in a given case where the probable error works out at 1 the average deviation is 1·183, and the standard deviation is 1·483. Consequently, in carrying out any particular investigation it is necessary to use the same method throughout in order to get strictly comparable results.

# CHAPTER IX

## THE EXPERIMENTAL STUDY OF INHERITANCE: SUMMARY

Our knowledge of the facts of inheritance has increased during the last quarter of a century at a rate incomparably greater than ever before, by the systematic carrying out of experiments on breeding. This era of activity in this particular line of research was inaugurated by the botanists. Hugo de Vries, a great Dutch botanist, as a result of crossing experiments on the Evening Primrose (*Œnothera*) hit upon a general principle of what he termed the " splitting of hybrids ", and practically at the same time similar results were reached by the German botanist Correns and the Austrian botanist Tschermak. On searching through the literature of the subject De Vries found to his surprise that his main results had been anticipated more than a quarter of a century earlier by Gregor Mendel, lecturer on science at Brünn in Austria, and afterwards Abbot of the Augustinian monastery at that place. Mendel's results had been buried in the *Transactions* of the local Natural History Society, and remained there unnoticed and sterile until disinterred by De Vries.

Mendel's work consisted of a systematic study of the phenomena of inheritance in peas, as observed

by crossing together plants showing mutually exclusive characters—now generally known as allelomorphs (Bateson)—such as tallness and shortness, smoothness and corrugation of the seed-coat, greenness and yellowness of the pea. While Mendel's work rested upon pioneer work on crossing plants by Kölreuter, and while some of his observations of fact were forestalled by others, it was Mendel alone who, for the first time, grasped the general principles involved.

Being, as they were, in complete contradiction to current belief, Mendel's results excited the greatest interest and most lively controversy. Pushed by advocates of great ability and unrivalled rhetorical powers "Mendelism" became, for a time, the fashionable field of biological research. A vast amount of important data was gathered relating to the phenomena of inheritance, and not only was the truth of Mendel's observations amply confirmed but it was made clear that "Mendelian" inheritance was not a peculiarity of peas but that it was widely spread throughout the vegetable and animal kingdoms. In 1909 I committed myself to the opinion that "Mendelian" inheritance was probably universal, and that apparent exceptions would probably find a Mendelian explanation later, and to-day, in the light of fuller knowledge, the great majority of biologists would probably be prepared to subscribe to this opinion. What exactly is meant by Mendelian inheritance will be made clear most easily by giving one or two simple examples.

### Blue Andalusian Fowls [1]

The Andalusian, or Blue Andalusian, is a well-known type of fowl characterized by the bluish impression produced by its diluted black plumage. It is obtained by mating together a black fowl of a particular breed with a white fowl with greyish splashes. Starting from a pair of such parents the immediate progeny (called by Mendelian experimenters the "first filial generation", commonly contracted into the symbol $F_1$) are blue Andalusians (Fig. 31, $F_1$). Now if blue Andalusians are mated with one another the second filial generation ($F_2$) are found to be of three different types, and these three types in definite numerical proportions. Two quarters,[2] or half, of the total number of individuals are blue Andalusians like their parents, while the other two quarters take after one or other of their grandparents, one quarter being white and one quarter black.

If now the breeding experiment be carried on to the next generation ($F_3$) it is found that mating the blue Andalusians together produces exactly the same result as that obtained by breeding from the Andalusians of $F_1$, *i.e.* two quarters, or half, the individuals are blue Andalusians, one quarter are white, and one quarter are black. On the other hand, mating the black individuals together produces only black offspring, and mating the white together produces only white.

[1] Bateson and Punnett, *Report of the Evolution Committee of the Royal Society*, 1906.

[2] It will be understood that all such precise statements regarding the proportion of individuals are necessarily liable to be inexact when only a few individuals are considered. They approach nearer and nearer to literal exactitude, the greater the number of individuals concerned.

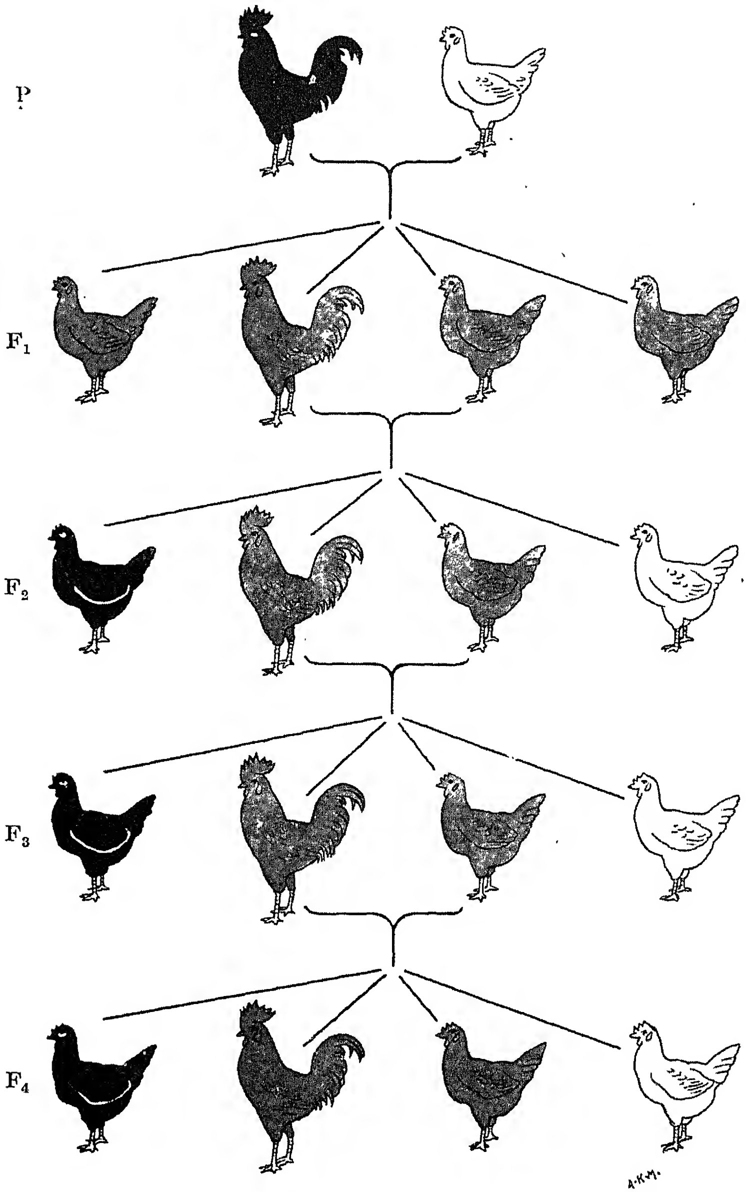



FIG. 31.—Mendelian inheritance in the Andalusian fowl.

By carrying on the experiment still further, through any number of generations, the same results would appear to be obtained, the blacks and the whites breeding true, while the blue Andalusians beget the three types in the "Mendelian" proportions of 1 black : 2 "blue" : 1 white.

## Guinea-Pigs[1]

As a second example of Mendelian inheritance I will take the case of the guinea-pig in regard to coat colour, the experiment being started by crossing a black individual of pure race with a white one (Fig. 32, P). In this case the immediate progeny ($F_1$) are all black. If now, however, such black guinea-pigs (*i.e.* $F_1$ individuals from a black × white cross) are mated together one quarter of the $F_2$ individuals are found to be white, and three quarters black. On mating together these black $F_2$ individuals it is found that although superficially alike they consist of two quite distinct types. One-third of them—*i.e.* one quarter of the whole $F_2$ generation (represented by the left-hand individual in the $F_2$ row of Fig. 32)—breed true. The remaining two-thirds, *i.e.* half of the whole $F_2$ generation, when mated together simply repeat a generation like their own—one quarter pure black, one quarter pure white, and two quarters superficially black but shown by subsequent breeding to contain a white strain latent in their being.

Now what are the general principles which emerge from such experiments?

[1] Castle, *Carnegie Institute of Washington, Publication No. 23*, 1905.

The experiment begins in each case by mixing together in the $F_1$ generation the two parental characters blackness and whiteness. By continuing the experiment to $F_2$ and subsequent generations these two characters are seen to separate or segregate out into distinct individuals. This is the Mendelian

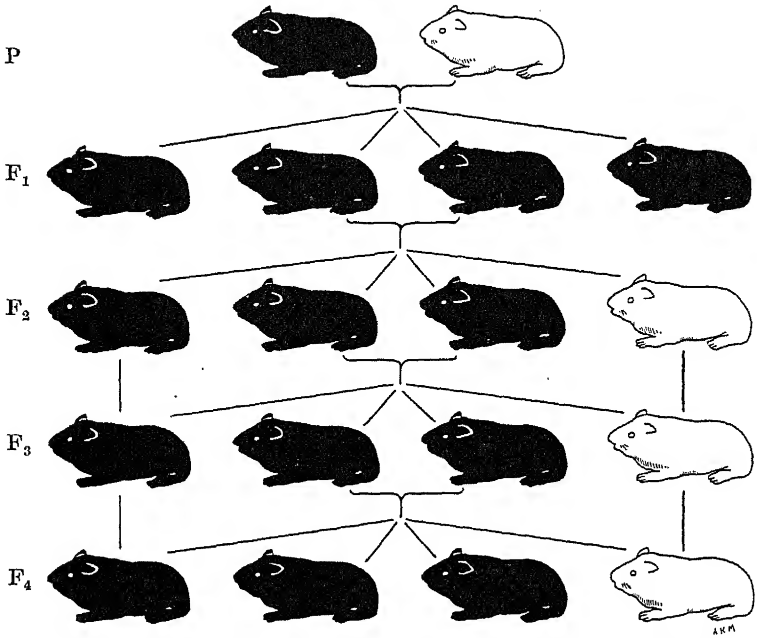



FIG. 32.—Illustrating Mendelian inheritance of black and white coat colour in the guinea-pig.

principle of **segregation**. These distinct individuals when mated together breed true, giving descendants all of their own colour. Their reproductive cells or gametes must therefore contain only the representative of this colour. This is the Mendelian principle of **purity of the gametes**. Finally it has to be noticed that, as regards the hybrid ($F_1$) generation of the guinea-pig experiment, where both blackness

and whiteness were present together in the constitution of the animal (see also two middle figures in each subsequent F row of Fig. 32) the whiteness was completely overborne by the blackness, these individuals being black and giving no indication of the whiteness which their progeny showed to be concealed in their constitution. Here we have the Mendelian principle of dominance; black is in this case said to be **dominant** over white, while white is said to be **recessive** to black.

It will have been gathered from what has already been said that Mendel and those who adopt the Mendelian method of investigation concentrate their study upon pairs of mutually exclusive characters. It is this intensiveness of their method which has yielded to Mendelian investigators their triumphs in the study of inheritance as compared with their predecessors.

The two examples I have given are sufficient to bring out the main features of Mendelian inheritance. For the sake of simplicity I have taken cases where only a single pair of allelomorphs is concerned.

We may now take a hypothetical case, where there are two pairs of allelomorphs, A and *a*, B and *b*, the dominant member in each pair being indicated by the capital letter, and plot out the possibilities after the manner devised by Punnett (Fig. 33). In this case each gamete of the $F_1$ generation will obviously carry the two allelomorphs in one of the four combinations, AB, A*b*, *a*B, and *ab*, and each individual gamete will have an equal chance of uniting in syngamy with any one of the four types. Thus if we write down the four types of egg in the vertical column we can place

on a level with each the four possible combinations with sperms. It will be seen that out of the sixteen possible combinations nine contain the two dominant allelomorphs A and B, three contain only the one dominant A, three only the dominant B, and one neither dominant.

Similar tables may be drawn up for combinations

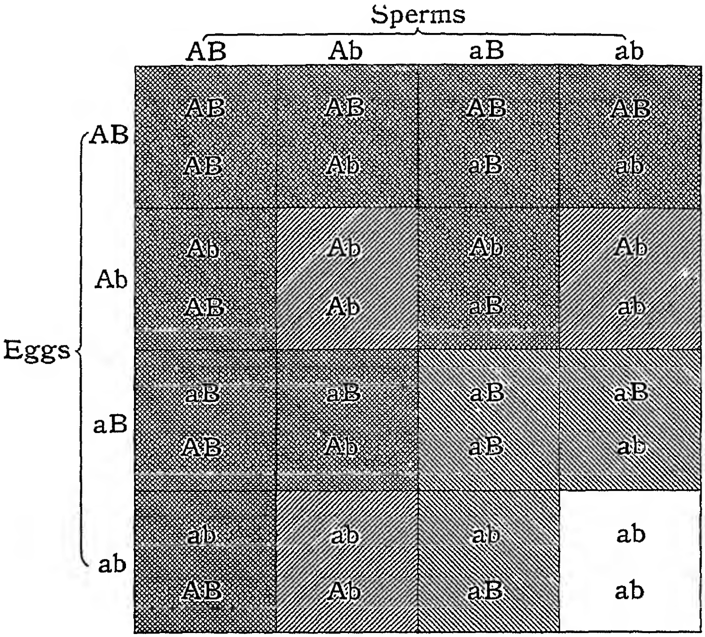



FIG. 33.—Diagram illustrating Mendelian inheritance of two pairs of allelomorphs—A and *a*, B and *b*—in the $F_2$ generation.

of three or more pairs of characters, and the results of actual experiment are found to agree on the whole with what such tables lead one to expect.

In all such cases the pairs of allelomorphs are considered as if they were entirely uninfluenced by one another. This assumption is a convenience in working, but it must be remembered that such

complete independence does not in all probability exist in the living body. In fact the trend of modern physiology is to show that the various characters of the animal body are intimately linked together, and none can be changed without causing change in others. In actual Mendelian work in recent years various cases have emerged in which it is clear that characters influence one another. For example, Bateson and Punnett found that crossing pure-bred fowls, one with a "rose" comb, the other with a "pea" comb, resulted in offspring with "walnut" combs.

### BOOKS FOR FURTHER STUDY

PUNNETT. *Mendelism.*
PUNNETT. *Heredity in Poultry.*
CASTLE. *Genetics and Eugenics.*
BATESON. *Mendel's Principles of Heredity.*

## CHAPTER X

### THE DIRECT CAUSE OF EVOLUTIONARY CHANGE

In the preceding chapters I have endeavoured to make clear why it is that those whose business it is to investigate such things are convinced (1) that a process of evolution has taken place in the past history of the animal kingdom, and (2) that the hypothesis of evolution has to be accepted as the true theory or working principle lying behind the manifold diversity of the animal kingdom as we see it to-day.

I have also given a sketch of the subject of inheritance, and have accentuated the fact of its failure to achieve completeness—the fact of variation—in which clearly must lie the basis of evolutionary change.

We are now confronted with the question: How has been, and how is, evolutionary change brought about? How do the comparatively small uncertain differences which distinguish the individual from its near relations become accentuated and fixed, to form the larger more constant differences which serve to separate species, genera, and groups of higher orders from one another?

It is clear that when we approach this question we penetrate into the realm of speculation. We can no longer hope to determine the true theory

with such certainty as to compel universal acceptance. All that we can do is to review carefully the knowledge of the day, to consider what possibilities suggest themselves, and, if there be more than one, to endeavour to make out in favour of which is the main weight of evidence and argument.

When we do this it is perhaps liable to cause surprise that we find only a single suggested explanation of evolutionary change in the animal kingdom that can establish its claim to be rigidly scientific, in making use of no factors that transcend actual observation and experience, namely, the hypothesis of natural selection. Doubtless this idea must have occurred to many previous naturalists, just as it occurred almost synchronously to Wallace, but it was Darwin, while elaborating his gigantic edifice of evolutionary philosophy, who alone grasped the full significance of natural selection, and saw how potent a factor it must necessarily be in producing evolutionary change.

Darwin leads up to the idea from the study of domesticated animals. Taking such an animal as a pigeon, a fowl, a dog, he shows how the various breeds of these animals differ markedly from one another, the differences being often more striking than those which distinguish separate species, or it may be even genera, of wild animals from one another.

Take, for example, the various breeds of domestic pigeon. There are over 150 of these different breeds, and they show the most astonishing differences in size, shape, colouring, relative size of bill and legs, plumage, and even in the internal organs, *e.g.* the Tumbler, with its abnormal brain mechanism which causes it to turn somersaults. These

differences are often much greater than those which separate different species of wild pigeon; they affect characters which may as a rule in nature show remarkable uniformity, as in the case of the Fantail, with its forty tail-feathers (rectrices) instead of the otherwise remarkably constant twelve.

And yet it is regarded as certain that all these breeds—the number of which every now and then receives an addition—have evolved from a single ancestral type, the Rock-dove (*Columba livia*)—the wild pigeon with the two dark bars across its wing seen commonly about the sea-cliffs of our coasts.

A cause which explains satisfactorily the differences between such breeds of domesticated animals might clearly be adequate to explain the differences between wild species.

But it is *known* how the breeds of domesticated animals have been made to diverge from one another. It is through the process of **selection** carried out by the breeder. The breeder has in his mind's eye a picture of the direction in which he desires to mould the breed. He carefully examines the available individuals, and isolates for breeding purposes those that show a leaning in the direction wanted. Those whose variation is in other directions—probably by far the greater number—he excludes from breeding. By continuing this process generation after generation he gradually brings about a modification of the breed in the desired direction.

Now Darwin asks: Is there no process going on in wild nature corresponding to this voluntary selection by which the breeder brings about evolutionary change in the case of his domestic animals?

He answers this question in the affirmative;

he shows that under wild conditions animals are necessarily subjected to a process which he terms **natural selection.**

(1) The individuals of a wild species tend in time to multiply greatly and so to outrun the means of subsistence.

(2) They do not, however, in fact, in normal circumstances, actually outrun the means of subsistence; on the contrary they, as a rule, remain roughly constant in number over prolonged periods.

(3) This implies that there is a relatively enormous death-rate, the whole progeny of a couple of parents on the average disappearing with the exception of a single pair which take their place.

(4) This death-rate is necessarily selective, inasmuch as, on the whole, if large numbers are considered, chance will favour those individuals that are fittest to survive, those that are adapted most accurately to their particular mode and conditions of life for the time being, while, on the other hand, it will act against those that suffer from any disability. The first lot will tend to live longer and leave more descendants, the second lot will tend to die earlier in life and to leave fewer descendants. And by the action of heredity the first lot will, on the whole, tend to transmit their fitness to their descendants, while the second lot will tend to hand on their handicap of disability to such progeny as they may leave.

The necessary consequence of these facts, says Darwin, will be that in nature a species is forced to undergo a slow evolutionary change in the direction of better and better adaptation to its surrounding conditions. As, naturally, these conditions are liable in course of prolonged periods of time to

change to an unlimited extent, either through their altering in themselves in response to climatic or other changes, or through the animal changing its home from one set of conditions to another, it would appear that if natural selection produces evolutionary change at all it may do so to an unlimited extent.

Such is in bare outline the hypothesis of natural selection. That it is a true theory is undoubted. That natural selection *does* take place and that evolution *must* be brought about through its working is beyond dispute, but as regards the proportional amount of such to the sum total of evolutionary progress there are current very different opinions, as is indicated by the fact that writers have felt themselves able on the one hand to claim the all-sufficiency of natural selection as an evolutionary factor, or on the other hand to claim that the theory of natural selection is, as an explanation of the evolution of species, "as dead as the Dodo". While the one would regard natural selection as sufficient by itself to account for the entire process of evolution in the animal kingdom through the variations which form the raw materials for its action, the other would regard the rôle played by natural selection as so relatively insignificant as to be negligible. In view of such discordant voices and in view of the difficulty in the way of those who not being themselves experienced zoologists have no means of knowing to what extent the proved reliability of his scientific work justifies weight being attached to the words of a particular writer, I will now examine in more detail the natural selection theory as it should in my opinion be formulated at the present day. This will involve occasional modi-

fications of the theory as originally formulated by Darwin, but such modifications are merely in detail, and do not affect the general principle.

## Evolutionary Time

It is desirable when considering the method of evolution to disabuse our minds of certain prejudices. One of these is the tendency to bring our ideas of evolution into relation with our ideas of the duration of time.

Every now and then the attempt is made by a physicist to put a limit to the extent of past time available for the evolution of the animal kingdom. We are, as I believe, justified in ignoring all such attempts, as being based upon foundations which are entirely inadequate. The observations upon which they are based may be of the highest degree of accuracy, the mathematical processes by which they are elaborated may be entirely beyond reproach, but there never can be any assurance against the existence of some factor, as yet unknown but vitally important, which will entirely invalidate the conclusion.

The most famous of such attempts to limit evolutionary time was that of Kelvin, who, on the basis of temperature gradients in the earth's crust, worked out the approximate rate at which the earth is cooling, and so was able to arrive at a period of years before which the earth would necessarily be at too high a temperature for living things to exist. Not so many decades after these calculations had been made came the discovery of a new factor—in this case the presence of radio-active materials in the earth's crust—and

the whole edifice of argument at once crumbled to the ground.

It is obvious that in dealing with physical processes on such a vast scale in the past history of the earth there never can be any certainty, or even probability, that all the important factors involved are known and their relative importance determined. We are consequently, in my opinion, entirely justified in refusing to allow our ideas of evolutionary time to be delimited in any such way.

The same consideration, which renders worthless all attempts to place a limit upon the entire period of evolutionary time, also invalidates attempts to estimate the duration of particular portions of evolutionary time, such as the length of time represented by a particular geological formation, or the period of time that has elapsed since a particular evolutionary event. The student of evolution must in fact take particular care to free his mind from the ordinary prejudices regarding the factor of time arising from our familiarity with such little time units as days, years, centuries, which, while full of meaning in the affairs of everyday life, are simply meaningless in relation to secular processes.

While he must disabuse his mind of the tendency to correlate the passage of evolutionary time with definite time units he must, on the other hand, realize that the process of secular evolution is one of extreme slowness. The period of a man's lifetime, in fact the period of human history, is merely as a lightning flash in the eternity in which evolution takes place. Consequently it is, as I believe, quite unwarrantable to suppose that we ought to be able to discern secular evolution making visible

progress before our eyes. The fact that we do not see such visible progress means, as I have already tried to emphasize, no more than does the fact that when, on a pitch-black night, we look out on a storm-tossed sea illumined by a single lightning flash we see the waves apparently motionless. It would seem to betray a singular lack of sense of proportion to suppose that failures to obtain positive evidence of evolutionary change from laboratory or breeding experiments carried on through a brief period of years—or indeed decades or centuries—can have any bearing whatever upon the question whether or not such change is actually in progress.

### Variation

It seems clear that the actual foundation of the evolutionary process lies in the fact of variation—the fact that the power of heredity is not sufficient to control the instability of living matter so completely as to ensure that the offspring shall be an exact replica of the parent, or of the mid-parent, or of the racial mean. On the contrary, in all their details, whether of structure or function, successive individuals show variation, now in one direction, now in another. Such divergences differ in range, those of wider range being, on the whole, rarer in rough proportion to the degree of their divergence. Very pronounced variations from the normal are liable to be inconsistent with continued life, and consequently to play no possible part in evolution. If consistent with life ("sports") they may be conspicuous and so attract attention, but to the present writer the balance of probability appears

still to be on the side of their being of little account in evolution, firstly on account of their comparative rarity in nature, and secondly on account of the liability of individuals possessing them to be handicapped by being out of joint with their surrounding conditions.

As variations differ in their range, so also they probably differ in the degree of their inheritability. Or, looking at the matter from a slightly different standpoint, different individuals differ in their power of passing on any particular variation to their descendants. On the other hand, I do not think there is sufficient justification for the view, urged especially by De Vries and his followers, that variations are divisible into two sharply marked categories: (1) those that are heritable ("mutations"), and (2) those that are not ("fluctuations").[1] It will of course be realized that proof of the actual existence of these two fundamentally distinct types of variation would be of much importance to the theory of evolution, for it would mean that the ordinary fluctuating variations that occur so frequently would be ruled out as factors in evolutionary change, and the latter would be dependent upon the possibly much rarer mutations. However, as already indicated, I do not feel there is any sufficient reason for giving up the view that variations are not divided into these two fundamentally distinct classes, but that they simply vary in the degree of probability of their reappearing in the progeny.

[1] The reader will not fail to bear in mind that "impressed" characteristics are excluded from discussion for the reasons stated in Chapter VI. Among such are to be included all peculiarities of the individual induced by circumstances or incidents during his lifetime. Such may closely simulate true variations, and hence are liable to be mistaken for them.

## Death and Selection

We have next the basic fact of the constancy of the population—the fact that on the whole the number of individuals of a given species in a particular area remains roughly the same from year to year. We do not, as a rule, see startling changes taking place during short periods of time although the particular species is reproducing actively. A single pair may give rise to a million [1] young and yet no conspicuous change in the population of adults is noticeable—the one pair of parents being represented by a single pair of adults in the next generation. This obviously means that out of the 1,000,000 new individuals coming into existence 999,998 on the average die, and two alone survive to replace the parents. Such large figures are impressive, but a little simple arithmetic will bring out the fact that even in a comparatively slowly breeding animal the death-rate must be high to keep the population down to anything like constancy.

It is equally obvious that this death-rate must be on the whole selective. It would be admittedly ridiculous to suggest that weaklings, or individuals whose variation is of a disadvantageous kind, will not thereby be handicapped, will not thereby have their chance of living through the mature period and leaving a full family behind them lessened. There necessarily *must* be **elimination of the less fit**, or, as Spencer put it, "survival of the fittest", or, as Darwin worded it less happily,

[1] Sometimes a far greater number. In the case of the Ling (*Molva vulgaris*), according to Fulton, a single female produces about 28 millions of eggs.

"natural selection". And if this be so, and if, as is the fact, heredity tends to pass on the particular kinds of fitness and unfitness to subsequent generations, then there is bound to be a slow progress of the race towards greater and greater fitness to their environment for the time being—in other words, a gradual process of evolutionary change.

It has then to be recognized that the struggle for existence, and natural selection, are actual facts which no one can reasonably dispute.

### The Potency of Natural Selection as a Factor in Evolution

Granted that the struggle for existence and natural selection are real and not imaginary things, we have now to consider to what extent they are really potent as instruments of evolutionary change. Unfriendly critics of Darwinism take, as a rule, the line of admitting their existence, but belittling their power. In my own opinion the attempts to do this have commonly been given far greater weight than they deserve. We have to remember that natural selection, the struggle for existence, the survival of the fittest, are phenomena of live animals existing under wild conditions. Their study is a branch of field natural history, and their founder, Charles Darwin, was a field naturalist of the highest qualifications. The further elaboration of these ideas and the final determination to what extent they require modification will be brought about by the studies of field naturalists, properly equipped with high technical training, who are willing to settle down in the tropics for pro-

longed periods, not with the immediate idea of confuting or supporting Darwin, but with the idea of "patiently accumulating all sorts of facts which could possibly have any bearing on" the problem.

No doubt the greatest triumphs of modern zoology have been achieved by research in the laboratory, but that does not mean that even the most skilled laboratory worker is necessarily qualified to form a reliable judgement regarding such matters as natural selection and the struggle for existence. Many of the attacks on Darwinism have emanated from the laboratory or the study, and for the reason indicated deserve far less attention than they have received. Certainly in my own case I found this type of criticism far more formidable in appearance at first than later on after I had had the intensity of the struggle for existence borne in upon me by actual experience in the tropics. It is, I think, a sound principle when assessing the degree of importance to be attached to criticisms which minimize the intensity of the struggle for existence to ascertain to what extent they rest upon extensive experience in the field.

Another point that it is necessary to bear in mind is that the natural selection hypothesis provides a suggested cause or explanation of evolutionary change, but that it makes no pretence to offer an explanation of the cause of variability. It simply accepts variation as a fact, and it is therefore quite unfair to bring against natural selection—as is often done—the criticism that it fails to explain variation—a phenomenon which it has never set out to explain.

As has been made clear in the earlier pages of

this book, I take the fact of variation—or, as I prefer to regard it, the *incompleteness of inheritance*—as one of the expressions of that general instability and inconstancy that is a fundamental feature of all living substance. It is, I believe, as much outside the scope of present explanation as is the nature of life itself. Although it is not possible to offer any explanation of its real nature it is important to realize that variability is in itself a feature of selective value. It is in fact a most important part of the equipment of the species for grappling with new sets of conditions, whether due to changes in the external conditions themselves or to changes in the habits of the animal whereby it brings itself into relation with new sets of conditions. Without variability the position of the species amidst changing conditions would be as impossible as that of a bicyclist with his front wheel clamped so that he could not vary his course from side to side.

It follows that although natural selection does not originate variability it does serve to foster and encourage it. Not only so, but we must realize that any particular variation is the outward expression of a *tendency* in the organism to vary in that particular direction. The selection of individual variations in a particular direction involves therefore selection of individuals *tending* to vary in that particular direction, and as a consequence the encouragement and intensification in the race of a tendency to vary in that particular direction. In this way natural selection will have a directive action upon variability, causing it to tend along particular lines. As a moving piece of matter, in accordance with Newton's First Law of motion,

tends to continue moving in the same straight line, so a selected strain of varying organisms will tend to keep on varying in the same direction.

### Intensity of the Struggle for Existence and its Effect in eliminating the less fit

Even in the absence of actual experience of the struggle a simple calculation, such as that on p. 137, is sufficient to convince any unprejudiced person that there *must* be in nature a struggle for existence of the most frightful intensity between animals occupying the same niche in the environment. The whimsical suggestion has been made that many animals are most crowded in the egg stage of their development, and that consequently if there is anything in the struggle for existence they ought to show a higher degree of evolutionary development in the egg stage than in the adult! Of course, as a matter of fact, the struggle for existence is nothing like so intense in these early stages of development, their needs being far simpler, and the most important of these needs—the need of the organism to find food for itself—being commonly met by the existence of a store of food-material hoarded up within the substance of the egg, or by its living as a parasite in the body of the parent. In a large proportion of animals the egg stage is in fact particularly self-contained, its needs being adequately met by little more than a supply of the necessary oxygen, provided the ordinary purely physical conditions, such as temperature and so on, are all right.

To learn by experience the intensity of the struggle, all that is necessary is to have to keep

oneself alive for a few months in the hostile environment of a wild country away from the resources of civilization. To any one whose fortune it has been to undergo this training it is indeed astonishing to hear those without such practical experience suggest that the struggle for existence is a much-overrated phenomenon.

And so also with the survival of the fittest, or to put it better, the elimination of the less fit. Those without actual experience often fail completely to realize how small and trivial a disability is liable under wild conditions to mean all the difference between life and death. To a human being in the wilderness, depending for food upon what he can get by hunting, a sprained ankle may mean almost certain death.

Memory recalls an occasion in the Gran Chaco when I fired at a Caraú (*Aramus*)—a strange somewhat Rail-like bird—as it flew overhead. Dissection later on showed that a single small pellet of shot had penetrated into one of the large pectoral muscles. It was, however, a long shot, and I thought the bird was undamaged; it continued its flight, to my eyes apparently without check or change. Not so, however, to sharper and more skilled eyes than mine; it had not gone more than a few yards when it was struck down by a large hawk, observant, no doubt, of some tiny change in its flight betraying its disability.

During the early settlement of the treeless pampa region of South America it was customary for purposes of shelter to establish large plantations in the neighbourhood of the estancia houses. An interesting sequel to this was the gradual penetration into the pampa of forest birds from the wooded

regions to the north. Amongst the immigrants into one of these plantations where I dwelt for a time were a pair of the beautiful scarlet-crested South American Cardinal finch (*Paroaria cucullata*). They had a family of young which had left the nest some little time before, and I noticed that these, with their conspicuous scarlet heads, were a source of irresistible attraction to the numerous half-wild cats which frequented the plantation. Eventually the cats got them all except the two parent birds, and I was assured by the estancieros that this was the ninth season in succession that the same thing had happened. Brood after brood was completely destroyed through the handicap caused by the brilliant red head. It might be that the scarlet crest of the cardinal carried with it in its original home and natural environment some unknown advantage, but it seemed equally clear that in its new environment it was on the whole a serious handicap, a factor of unfitness leading to elimination. And the conclusion seemed unavoidable that had any of the young cardinals failed to develop the scarlet feathers on their head they would have thereby acquired a greatly increased chance of surviving and transmitting their peculiarity to increasing numbers of descendants, so that in time a new species characterized by the absence of the scarlet crest might evolve in this manner.

The fact is that to the naturalist experienced in the study of wild nature in her haunts, remote from the disturbing influence of man and his civilization, it is amply apparent that the poet's word-picture of "Nature, red in tooth and claw with ravine" is a perfectly correct one. Wild nature—especially in the tropics, the great workshop of evolution—is

an intense and pitiless struggle in which the less fit are ruthlessly eliminated and the mean of the race maintained in that way at the highest level of efficiency in relation to the surrounding conditions of the moment.

A type of argument against natural selection, which, although in my opinion entirely fallacious, has attracted a good deal of attention and still frequently makes itself heard, is that which considers individual organs or parts of organs by themselves, apart from the organism as a whole of which they form a part. Taking some highly developed complicated part of the animal body, it is argued that it could have evolved, according to Darwinian ideas, only if all the various parts of which it is composed happened synchronously to present variations in the proper direction, for natural selection to make use of. In the neck of the giraffe each one of the seven vertebrae must have varied in the same direction at the same time. In the eye of a vertebrate the several components—lens, retina, vitreous, cornea, choroid, sclerotic, and so on—must each one of them have varied, and kept on varying, in the proper direction, just at the proper time, to ensure each becoming properly adapted to fit in with the others as parts of the complete organ. The fallacy underlying this argument is that nature selects not separate organs, or parts of organs, but whole individuals.

It is becoming more and more clearly recognized that the individual animal is to be regarded primarily not as being built up as an aggregation of separate parts, but rather as a physiological whole, which for greater efficiency is more or less subdivided into parts. These parts remain in physiological

continuity: they are intimately linked together in the organization of the body, and variations of any particular part or organ are to be regarded as variations of the individual, showing itself in the particular part rather than as variations of a self-contained and independent structure or organ.

The same fallacy crops up in another form. Small variations, small departures from the normal, are naturally more frequent than large ones. I have used the expression normal, but actually no individual is absolutely normal. What in ordinary language we call a normal individual is one in which the variations from the mean are not large enough to attract attention. Every individual possesses these minute variations; rare individuals vary in such a way as to be quite conspicuous. The Darwinian theory of natural selection regards the larger, rarer variations as of less importance in evolution than the smaller, more frequent variations. Critics, however, suggest that this leads to an impasse, for, they say, *small variations can have no selective value.* Here again they are being led astray by allowing their attention to become concentrated on isolated characters or organs. As a matter of fact a very large difference in the efficiency of the individual as a whole may be brought about by a variation in a particular organ which seems quite trifling if one restricts one's vision to that particular organ rather than to the individual as a whole. For example, a slight variation in the activity of one of the ductless glands may result in the most startling difference in the disposition or health and consequently in the efficiency of the individual.

Still one more fallacious criticism of natural

selection must be attended to, namely, that it cannot account for the *beginnings* of any organ, seeing that in its incipient stages an organ must be useless. This argument is invalidated by two different considerations. Firstly, by the general consideration set forth in the preceding paragraph, for it relates to particular bits of an animal taken by themselves. But it is also invalidated by this further consideration, namely, that an organ does not arise in evolution out of nothing. An organ is a part of the living substance of the body in which some one or more of the general functions of living substance becomes exaggerated, so that, as compared with other parts of the body, it is responsible, mainly or entirely, for the carrying out of that particular function.

In the more complex animals one does not suppose for a moment that a "new" organ really arises *de novo*. On the contrary, it arises by gradual change in function and structure from some preexisting organ. For example, the wing of the bird unquestionably evolved out of the reptilian foreleg. In seeking the solution of an evolutionary problem in which I am particularly interested, that of the evolutionary origin of the limbs of vertebrates in general, it never occurred to me to suggest that they had come into existence out of nothing. On the contrary, the problem resolved itself into the question: What organ could be found belonging to an earlier stage of evolution which might reasonably be regarded as likely to have undergone the slow modifications in function and structure necessary to convert it into the limb?

I think I am justified in stating that such would be the mental attitude of any competent morpholo-

gist in tackling the problem of the evolutionary origin of an organ. It is to raise quite imaginary difficulty to say that the incipient stages of an organ are useless.

Natural selection as an evolutionary factor being concerned primarily with bringing about a more intimate adaptation of the animal to its environment the question naturally arises: To what extent are the peculiarities that serve to distinguish the different types of animals from one another of such a nature as to play a part in fitting them to their environment? In other words, To what extent are animal characteristics adaptive or useful, and consequently of such a nature as to be fairly attributable to the direct action of natural selection? The next chapter will deal with the consideration of this question.

BOOKS FOR FURTHER STUDY

DARWIN. *The Origin of Species.*
POULTON. *Essays on Evolution.*

# CHAPTER XI

## ADAPTATION AS ILLUSTRATED BY THE COLORATION OF ANIMALS

As a means of making clear to the reader the extent to which the principle of adaptation pervades the characters by which we distinguish the various members of the animal kingdom from one another I will, in this chapter, make a general survey of the coloration of animals. Animal coloration is peculiarly suitable for driving home such a point as this, in the first place because it is one of the conspicuous characteristics by which many of the most familiar animals are differentiated, and in the second place because the facts involved can be fully appreciated without any specialist training.

A broad survey of the animal kingdom shows that, as a very general rule, the colouring of animals serves an obliterative function: it tends to render the possessor inconspicuous when in its natural surroundings.

If we consider the method by which, in ordinary circumstances, we recognize a particular object by the eye it becomes obvious that there are three factors concerned in bringing about this recognition: (1) **Colour**—the object forms a patch of colour which stands out in contrast against the background; (2) **Outline**—the particular object has a

regularity or familiarity of outline which again distinguishes it from the different objects which surround it; (3) **Relief**—the object, or parts of the object, stands out more or less distinctly in solid relief.

If now we turn to the coloration of animals we find obliterative effects produced by the nullification of each of these three factors:

### I. Thayer's Principle—the Disguise of Relief by Countershading

In Fig. 34 is shown a pure white fowl against a pure white background, lighted by ordinary daylight from the sky in the open. One might have expected that a pure white bird would be invisible against a pure white background, but the picture shows that this is not the case. The fowl is quite conspicuous. And a little inspection of the figure shows clearly why it is so. Although the plumage is actually white it is seen that on the lower side of the body the white is reduced to a deep grey owing to its being in shadow: this side of the bird is rendered quite conspicuous against the background by its apparently darker shade. On the other hand, the upper side of the bird also stands out conspicuously from the background, owing to the high light giving it a special brilliancy. As a matter of fact it is only the parts of the bird's surface that are approximately vertical that appear to be of exactly the same shade as the background; those parts which slope in underneath the bird are in deeper and deeper shadow; those, on the other hand, that slope upwards towards its back come into higher and higher light.

This light and shade effect, so well illustrated by the case of the white fowl, is one of the chief factors in causing the appearance of relief in nature, and one of the most striking principles of animal coloration is that by which in the case of wild animals the working of this factor is nullified by beautifully graduated countershading.

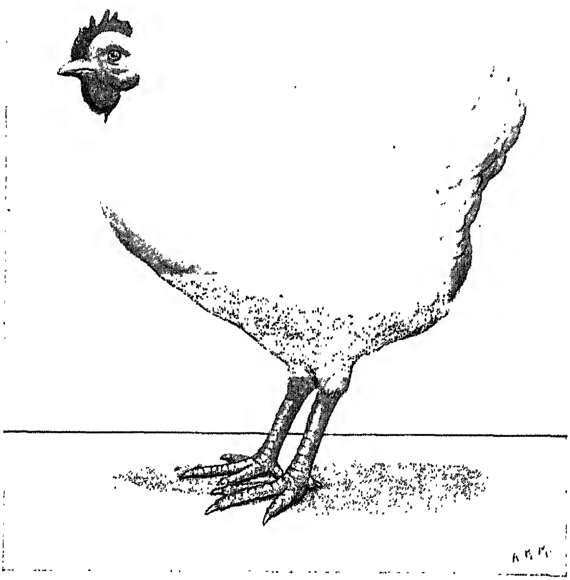


FIG. 34.—White fowl as seen against white background.

This principle of animal coloration was first grasped by the American artist Abbott H. Thayer, and the writer of this book will never forget his experimental demonstration of his principle in the London Zoological Gardens some twenty-five years ago. Thayer made use of a couple of roughly modelled ducks covered with sackcloth. Placed in the open against a background of sackcloth they

stood out distinctly, for the same reason as the fowl in Fig. 34. The artist then set to work with his paint and brushes on one of the models and in a very short time it had completely vanished from view. Tilting the model slightly out of position so as to alter the incidence of the daylight at once destroyed the illusion, but restoration to the position in which he had painted it caused the model again to disappear. On now proceeding to examine at close quarters the model which Thayer had painted it was at once obvious that it had assumed a type of shading familiar in wild animals. The back had been darkened in shade — just sufficiently to counteract the high light from the sky—the under surface had been whitened—to counteract the deep shadow—and between these two extremes the shading had been nicely graduated, only the central portions remaining untouched.

This principle of Thayer's is seen exemplified in many different types of wild animal where the dark line down the back, the white belly and the graduated shading between go far to destroy the roundness and reduce its appearance to a flat smudge. Although the principle was first formulated in modern times by Thayer, I was interested some years ago, when examining some ancient Chinese paintings, to notice that it had been apparently fully grasped by Chinese artists several centuries earlier.

### II. Blurring of Outline

It is only in comparatively small animals that the breaking up or blurring of the tell-tale regularity of outline is practicable. In some fish and insects this is achieved by the body-surface growing out

into irregular projections: in the case of young birds or small mammals a blurring of the sharp outline is effected by the down feathers or the fur (Fig. 35). In various birds the outline of the head is disguised by the presence of a crest, and in the wild Indian the same effect is produced artificially by wearing a crown of feathers.

FIG. 35.—Curlew chick.
(From Thayer: photograph by C. and R. Kearton.)

### III. Breaking up of Continuity of Surface: "Dazzle" Patterns

Another beautiful principle which nature makes use of is that which has come to be familiar from its war uses under the name "Dazzle".[1] In this she takes advantage of the psychological processes which are made use of in the act of recognition, inasmuch as she superimposes upon the surface of the animal's body conspicuous

[1] As representatives of the British Admiralty have called in question my attributing the prior use of this term to Thayer, I give the reference: *Concealing Coloration in the Animal Kingdom*, New York, 1909, p. 152, etc.

markings, which serve to concentrate upon themselves the observer's attention, and in this way enable the tell-tale colour or form of the animal to pass unnoticed. The principle is the same as that which makes an open lace-work curtain, or even an arrangement of white tapes pinned at considerable intervals across a window, effective as a means of preventing the casual passer-by from noticing the interior of a room. If his glance rests upon the window his attention is forcibly concentrated by

FIG. 35.—Inspection from a little distance in a dull light shows that the left-hand figures are rendered less readily recognizable by the conspicuous dark marks imposed upon them.

the curtain pattern, and he notices nothing of what is beyond it. That the curtain acts in this way and not as an ordinary opaque screen is easily shown by dyeing a portion of the curtain black, when it at once loses its efficiency as a screen. Even the lesser diminution in conspicuousness of the lace-work, due to the darkening in colour through the accumulation of dust, is seen to diminish the efficiency of the curtain.

The working of the "dazzle" principle is illustrated by the simple diagram shown in Fig. 36.

The corresponding figures are shaded to exactly the same tone, then on one of each pair has been superimposed a conspicuous mark, and it will be noticed, by looking at the book from a little distance, that the figure so treated has become less conspicuous than its fellow. Amongst animals we find this principle frequently at work, rendering them less conspicuous in their natural surroundings.

In Fig. 37 the fish (*Anisotremus*) are seen to

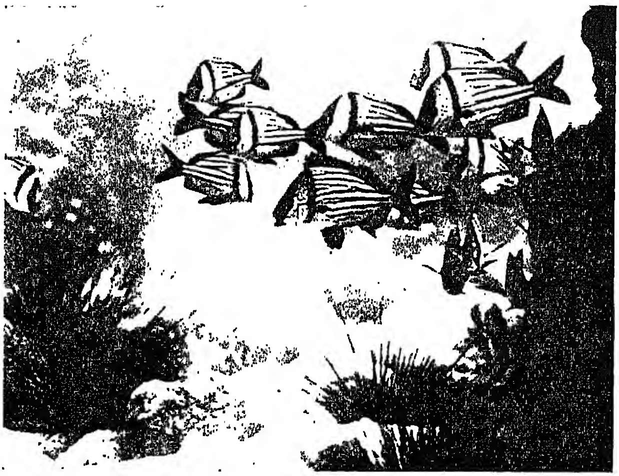


FIG. 37.—*Anisotremus virginicus*, a Tortugas fish. (Photographed by Professor W. H. Longley.)

show a dark and light striping which effectively breaks up the continuity of their surface.

In Fig. 38 the surface of the toad is cut in two by the pale line: it is this line which is noticed as the glance travels over the natural surroundings of the animal, and it fails entirely to call up the mental picture of a toad.

In Fig. 39 the continuity of the surface of the young grebes is broken up by the conspicuous light and dark patchwork, which fails entirely to suggest

the body of a bird to the eye glancing casually upon the grebes amid their natural surroundings. Simi-

Fig. 38.—A South American toad, *Bufo typhonius*.
(Photographed by Mr. J. F. M. Floyd.)

Fig. 39.—Young crested grebes.
(From Thayer: photograph by C. and R. Kearton.)

larly, in the case of the woodcock shown in Fig. 40 the heavy dark and light markings fail completely to

FIG. 40.—American woodcock on its nest. (From *Concealing Coloration in the Animal Kingdom*, by Gerald H. Thayer.)

suggest to the passing glance the form of a bird.

Admirable examples of this principle occur among the larger mammals. A zebra, or giraffe, or leopard, or jaguar is familiar to the visitor to a museum or menagerie by the extreme conspicuousness of its black and yellow markings. In their native wilds, however, in the dusk or in moonlight—the times that the larger carnivores are most active—these animals are quite extraordinarily inconspicuous when they remain absolutely motionless, as they do when desiring to escape notice.

## Isolated Distractive Markings

The ordinary "dazzle" type of coloration has been compared in its mode of action with a white lace-work curtain across a window: it serves to concentrate the attention of the observer upon itself, so that more important things are missed.

We find the same principle exemplified by isolated marks upon the animal's body, which serve

to concentrate attention upon themselves rather than upon more vital features.

Beasts of prey very usually tend to attack other animals by striking at their head end, no doubt because that end of the body (1) goes first in the more active movements ; (2) encloses the brain and eyes, by injury to which the animal can most readily be incapacitated ; and (3) bears the jaws, in many cases the chief defensive weapons. A bird, for example, when attacking a smaller animal will very commonly peck at the eyes. In correlation with this we frequently find distractive markings bearing the semblance of eyes present in such positions as to divert the attention of an enemy from the vital head end to some less important part of the body. Such eye markings are found best developed in the Lepidoptera, where "eye spots" are in many species developed in a position where they are far removed from the vital organs, *e.g.* round the margins of the wings. The attacking bird is attracted by these apparent eyes, and, pecking at them, merely lacerates or punches a piece out of the wing margin, while the animal escapes without any serious injury.

A still more pronounced expression of the same principle is seen in the case of various caterpillars, where the hind end of the body simulates a head: it may be by the possession of a pair of glaring eye spots, it may be by the presence of a pair of thin projecting filaments which simulate antennae.

Undoubtedly in some of these cases where a pair of conspicuous eyes are present, say, on the body of a large caterpillar or the wings of a large moth, they have attained a further use, that of calling up to the animal that glimpses them the

mental picture of some much larger and more formidable creature that had better not be interfered with.

### IV. Obliterative Resemblance to Background

This occurs in one of its simplest forms in the leaf-green coloration of many animals which live amongst green vegetation. In the case of parakeets, the green of the plumage matches the chlorophyll green of vegetation with such extraordinary accuracy that I have actually had difficulty in finding a specimen which I had brought down, even when I had marked the exact spot at which it reached the ground, until I felt for it with my hands among the grass. In various insects such as locusts, mantises and leaf-insects the matching is equally accurate, and the obliterative effect may be increased by the resemblance between the nervures of the wing and those of a leaf.

The reddish colour of many mammals and birds would appear also to be related to the green colour of the vegetation. I was led to realize this by an experience in South America when tracking down a party of Indians. To put difficulties in the way of following the trail the party of Indians had scattered, and there was some doubt on the part of the pursuers, when it suddenly became apparent that the margins of the forest along which the patrol was passing were crowded with Indians. They were seen only with the greatest difficulty, owing to the perfect manner in which their dark coppery skins blended with the dark shadows of the forest. These shadows are in fact not merely

dark: the skilled artist will sometimes realize that they assume a reddish hue through contrast with the green foliage, and it is this fact which gives an obliterative effect to the Indians' skin. In all probability the reddish hue of the fur of so many wild mammals is of distinct utility for the same reason.

Beautiful examples of obliterative colouring are afforded by the animals which live on the lichen-covered bark of the trees in tropical forests. Many years ago, on one of the South American rivers, I had a striking demonstration of this. As our small exploring steamer pushed its way along the narrow creeks its high upper works brushed against the branches of the overhanging forest trees, and our decks became soon littered with a mass of debris consisting apparently of lichen-covered twigs. We very soon began to notice movements in the mass and found that a large proportion of it consisted of living animals—snakes, lizards, frogs, spiders, scorpions, locusts, mantises, beetles—all coloured in such a way as to match with the greatest precision the lichens amongst which they had their home.

### Assumption of Obliterative Colouring in Response to Environment

In certain cases such obliterative resemblance comes about as a direct reaction on the part of the individual animal to the colour of the background, this reaction in some cases occurring only once in early life and producing a permanent effect, in other cases being repeatable and producing a temporary effect according to change of background. The former is well exemplified by the

pupae of certain insects such as our common cabbage butterflies (*Pieris*). In these butterflies the pupa or chrysalis is commonly slung up to the surface of a wall and usually is inconspicuous through its colour approaching that of the background. Poulton[1] has described a series of beautiful experiments in which he allowed the caterpillars to pupate in boxes with linings of different colours, and obtained in this way the most wonderfully accurate matchings of colour between the pupae and the lining of the boxes.

Many of the South American butterflies have on the under side of the wings a pronounced pattern of light and dark stripes or elongated markings so arranged that they are approximately vertical when the butterfly is in the resting position. I remember one chilly morning on the Pilcomayo river being quite startled by suddenly becoming aware that the still dew-laden grass all round was peopled by thousands of these butterflies clinging to the grass stems, the light and dark striping of their wings blending with the general light and shade effect of the grass so perfectly that I had missed them entirely up to that moment.

When wading in the reed-beds of the Pampa lagoons I had frequently occasion to observe the parallel case of the beautiful little heron, *Ardetta involucris*, with reddish-coloured plumage marked by dark stripes. When flushed it would fly away conspicuously through the reeds and then suddenly vanish, as Hudson[2] so graphically describes. When by very accurate marking of the exact spot at which it disappeared it was possible to detect the

[1] Poulton, *Transactions Entomological Society of London*, 1892.
[2] Sclater and Hudson, *Argentine Ornithology*.

heron again, it was found clinging to one of the reeds, its neck and bill stretched vertically upwards, and the striping on its body harmonizing exactly with the general light and shade of the reed-bed.

It should be realized that a high development of these various devices by which animals are rendered inconspicuous is commonly accompanied by psychical activities or "behaviour" which serves to increase enormously their effectiveness. The most striking of these is the assumption of absolute stillness on the part of the owner. It is a frequently recurring experience in wild nature to see an obliteratively coloured animal dashing away when one has inadvertently approached to within a few yards of it: when it bursts into movement it then becomes "visible" for the first time. To the hunter of wild game who has attained to considerable skill it occasionally happens that as he steals silently along the edge of the forest he suddenly becomes aware of a deer or other large animal standing absolutely motionless almost within touching distance and remaining so until it realizes that it has been detected. Again, animals with well-developed protective resemblance show a distinct partiality for the type of background which makes their scheme of colouring most effective.

Active and repeated response to change of background is found in many types among the lower vertebrates—such as fishes and frogs. Amongst fish particularly good examples are afforded by the Pleuronectidae or flatfish such as the flounder or sole. In these animals the granules of pigment in the skin are concentrated in special cells called chromatophores. Each chromatophore when functional spreads out so as to cover a wide area,

while at other times it is capable of contracting into a spherical shape so that the whole chromatophore now forms merely a tiny, hardly visible, dot which is quite without effect on the general colouring of the animal. In some cases the chromatophores contain only dark melanin pigment, and in such a case expansion of the chromatophores causes the animal to be black in colour, while their contraction renders it whitish and translucent. In various cases different sets of chromatophores contain pigment of colours other than black, and the expansion of those containing one colour combined with the contraction of those containing another bring about conspicuous changes in the general colouring of the animal. These changes are adaptive and come about in relation to the colour of the background. Thus a flatfish adapts its colouring in the most striking way to that of the sea bottom—sand, or mud, or gravel. Or a tree-frog may be of the most brilliant green when amongst green leaves, while it takes on a brown colour when placed against a brown background.

These colour responses are of much physiological interest. In some cases the reaction is a complex one involving a complicated mechanism of muscle and nerve and is set in action through the sense of sight: such is the case with the wonderful colour changes seen in the Siphonopoda (cuttle fish and squids). In other cases it is of a simpler and more direct nature, the chromatophores reacting directly to the light impression falling upon them. Many years ago I observed a beautiful demonstration of this in South America. I was watching a green tree-frog and admiring the wonderful way in which its colour matched that of the vegetation. It was

in bright sunlight and across its body ran the sharp shadow of a blade of grass. After watching it for a time the frog suddenly sprang some little distance —and it appeared to carry with it the shadow of the grass blade. In other words, the dark chromatophores situated in the shadow of the grass blade had passed into a condition of expansion so as to produce an actual band of darkness in the frog's skin, and it naturally took an appreciable time before this disappeared after the shadow which had caused it was no longer present.

## Conspicuous Coloration

While it is indubitably a very general rule that the colouring of wild animals in their natural surroundings is obliterative, it is obvious that there are many and glaring exceptions to this rule. In the case of coal-black tadpoles, or black and yellow wasps, or brilliantly coloured butterflies, it is obvious that the general effect is the very reverse of inconspicuousness. It is necessary then to inquire whether or not in such cases the colouring of the body has not some adaptive significance other than that of obliterativeness in the ordinary sense.

The colours of objects are of course due, unless they are self-luminous, to the reflection of the light which falls upon them. If this reflection is indiscriminate the object in ordinary daylight is white: if, on the other hand, it is selective, light of certain wave-lengths only being reflected, the object displays a colour corresponding to light of that particular wave-length. In the case of coloured animals the selective reflection is brought about by two main methods—(1) interference and (2)

pigmentation. In the first case reflecting surfaces are arranged in series, one behind the other, at such minute distances as to cause light waves of a particular wave-length to fit accurately between one another, thus obliterating the waves of that particular length so that the light actually observed as reflected from the surface is the residuum of the daylight after the particular wave-length or colour has been blocked out. Many of the most gorgeous metallic colours of birds' feathers or of insects' wings are produced by this process of interference, the serial reflecting surfaces being either superficial parallel ridges or thin superimposed layers of transparent material with reflecting surfaces between.

More usually, however, the colours of animals are due to definite pigments which absorb the light of certain wave-lengths and reflect that of others. These pigments differ much in the detail of their chemical composition, but in general terms they may be said to be waste products of the animal's living activities, which instead of being simply passed away to the exterior, as is the case with ordinary excretory materials, are retained in the body and deposited in insoluble form in its surface layers. There they carry out what is to be regarded as the primary function of skin pigment—the exclusion of the harmful rays of light from the delicate living protoplasm. Whereas the more primitive and lowly organized animal organisms lurk amidst the shadows, the more complex creatures enclosed in their light-proof garment of pigment are able to venture with more impunity into the open daylight.

The commonest type of light-excluding pigment functions simply by absorbing the light rays in-

discriminately: consequently it produces simply a dark effect. Such is the case with the dark melanin pigment of the human skin, seen in its highest degree of development in the beautifully efficient skin of the negro, or in the cells of the various types of visual organ, where it serves to protect the surrounding living cells from the intense light flooding the interior of the eye. A property of this dark pigment which must be of disadvantage in particular cases—such as that of the negro's skin—is that, while it blocks the light rays by absorbing them, it at the same time absorbs heat rays. This disadvantage is to a great extent avoided in the case of another type of light-excluding coloration, namely white. In this case the light is kept out not by absorption but by being reflected back from the body—the heat rays to a great extent also undergoing exclusion in the same way. The white colour in such cases is frequently produced by pigment—as in the case of our common white butterflies—in other cases it is caused by the presence of minute air-bubbles—as in the case of white hair in human beings and other mammals.

More usually the pigment does not reflect indiscriminately: it absorbs rays of certain colours and reflects the remainder, and in this way are produced the majority of the colours of animals.

In approaching the study of the conspicuous and brilliant colours of animals it is necessary to bear in mind that many of the excretory substances produced by animals happen to be brilliantly coloured chemical compounds. They happen to have brilliant colours, just as many chemical salts outside the animal body happen to have brilliant colours. Accordingly, if in a particular case the

excretory material deposited in the skin happens to be one of these brilliantly coloured substances, then the surface of the body necessarily takes on a brilliant colour, and the more intense its vital activity, the more intense its metabolism—and the greater the deposit of the resulting waste products in the skin—the more intense will be the brilliance of the colouring. Consequently the occurrence of brilliant colours on the surface of the animal body is to be regarded as *primarily* due to mere chance.

It is perhaps necessary at this point to utter a word of warning against being led astray in the consideration of this question of the colouring of animals by a potent disturbing factor, namely our sense of beauty. The naturalist, regarding some natural object, feels at times almost overwhelmed by his appreciation of its wonderful beauty of colour or form, and he is apt to forget for the moment that the beauty is not inherent to the object but exists in his own brain. According to his particular experience and education he projects the conception of beauty into the phenomena he observes. Had his past experience and education been different, so also would have been his aesthetic sense. When I encouraged wild Natokoi Indians to sniff delightful toilet scents they made grimaces of the most intense disgust!

When we make a general survey of those members of the animal kingdom that have a conspicuous scheme of coloration, we find in the first place certain cases in which we are justified in regarding brilliant colour as actually a matter of mere chance. Many years ago at Cambridge I was impressed by what is probably still the best

example of this, namely the brilliant red colouring which is frequently found in prawns from considerable depths in the sea. This was frequently alluded to in books on marine zoology, but no reference was made to the remarkable puzzle which this fact presented. A little inquiry was sufficient to dispel the mystery. It was clear in the first place that an object could be red only if it were illuminated by light which includes red rays. The feeble light at the great depths at which these creatures lived consisted partly of daylight filtered through the superjacent sea water, and partly of light given off by marine organisms. It was apparent from the evidence then already available —evidence confirmed and greatly amplified by the work of the "Michael Sars" Expedition[1]—that in this light there were practically no red rays. Consequently these creatures in their native home were not red at all: they were merely dark in colour: and it was consequently a matter of mere chance that when brought to the upper world with its daylight rich in red rays they took on a red colour.

In all probability, though not with the same certainty, the element of mere chance plays an important part in relation to the vivid colourings of butterflies and birds. In the case of birds the more homely and frequently obliterative colours of the female, in cases where the male is brilliantly coloured, is very probably due to the influence of natural selection in tending to eliminate characters that would render the incubating bird conspicuous. On the other hand, if the production of the brilliant colouring matters in the male be an index of its

[1] Murray and Hjort, *The Depths of the Ocean.*

vital activity it would tend to be accentuated by the same factor.[1]

Whereas in the cases so far alluded to the brilliant colouring is meaningless, or at least without any meaning obviously related to the environment, it is quite otherwise in the case of large numbers of animals in which the colour scheme is of such a nature as to make the owner readily recognizable. The majority of these are cases of **warning coloration**—the particular animal has some potent means of defence, such as a sting or an unpleasant odour or taste—and it is clearly to the advantage of its species that it should have a conspicuous livery easily remembered and recognized by animals that have had experience of attacking it and suffering the consequences. It is obvious that a child who interferes with wasps is very soon educated to avoid these conspicuously coloured insects.

Among the sea-snails (Gasteropoda) there is a special subdivision known as Nudibranchs in which the shell that normally protects the body of such animals has disappeared. Most of these creatures possess an efficient obliterative colouring, but there is one set of them, represented by the genus *Aeolis*, in which, on the other hand, the colour is glaringly conspicuous, and this colouring is found to be correlated with special defensive organs which are absent in the other members of the group. The body has projecting from its dorsal side numerous flabby club-shaped processes, and each of these has embedded in its tip a battery of the remarkable poisonous and explosive structures known as nematocysts—microscopic hypodermic syringes charged with virulent poison. The presence of these tiny

[1] See, however, Chapter XII.

weapons seemed in the early days of evolutionary science to form a serious obstacle in the way of accepting the idea of evolution, for, while nothing like them was known in other molluscs, they were seen to be identical with the nematocysts occurring in a far more lowly organized subdivision of the animal kingdom, namely the group Coelenterata, to which the sea-anemones and other polyps belong. Obviously the occurrence of *identical* organs in two widely separated divisions of the animal kingdom would not fit in with any system of natural evolution. Consequently it was of great interest when in 1903 Grosvenor resurrected and amply confirmed a long-forgotten discovery that the nematocysts of *Aeolis* were not manufactured in the body of that animal but were obtained from hydroid polyps on which the Aeolis feeds—digesting the protoplasmic parts but retaining the nematocysts and storing them up in the unexploded condition for its own use.

Good examples of warning coloration are found amongst the Amphibia, as *e.g.* in the black and yellow salamander of the Continent, or the little toad, *Atelopus*, of South America, with its brilliant orange markings. In each of these cases poison glands in the skin make the creature highly distasteful: a pet *Cariama* which I had in South America, and whose favourite diet consisted of frogs, would on no account have anything to do with specimens of *Atelopus*.

The skunk, with its conspicuous black and white fur and its horrible odour, is again a good example of warning coloration.

## Mimicry

Some of the most remarkable facts of animal coloration have to do with the phenomenon commonly known as **mimicry**. A preliminary general idea of the phenomenon may conveniently be got from the Lepidoptera (butterflies and moths). When a naturalist, collecting the butterflies of a particular neighbourhood in the tropics, comes to examine in detail the butterflies which he has roughly sorted out into their different species, he is liable to have an experience which, were he not prepared for it, would be very surprising. Among a large number of insects which he has put together as obviously from their general appearance belonging to the same species he finds a few specimens which, when examined in minute detail, are seen to belong to a different species from their companions. Not only so, but it may become obvious from the minute details of their structure that their species is far removed from that of the majority: they may belong to a quite different family of butterflies: they may even turn out to be not butterflies at all but moths—cunningly disguised as regards their general appearance so as to resemble the particular species of butterfly.

On Plate I. (Frontispiece) are seen accurate representations by Mr. A. K. Maxwell of a few typical specimens illustrating this phenomenon.

The upper pair (A) are two Indian butterflies. Although their general resemblance is extraordinarily close, the details of their structure show that they belong to quite different groups, the right-hand one (1, *Papilio agestor*) belonging to the Papilionidae or Swallow-tail family, while the left-hand one (2, *Caduga tytia*) belongs to the Danaidae.

In the second pair (B), from Sikkim, the left-hand one (3, *Papilio bootes*) is one of the Swallow-tail butterflies, while the other (4, *Epicopeia polydora*) is not a butterfly at all but a moth which has taken on the semblance of this particular swallow-tail butterfly.

In the third pair (C) the left-hand member (5, *Ithomia diasia*) is a typical example of a group of butterflies with small and inconspicuous wings, transparent owing to the fewness of the scales, which flit about unobtrusively in the recesses of the South American forests. Its fellow (6, *Gerra hyelesoides*) is not a butterfly but a moth which has given up its typical appearance and taken on the semblance of the Ithomia.

In the pair D the right-hand member (8, *Heliconius robigus*) is a typical example of the great South American family of butterflies known as the Heliconiides. These butterflies, with their long-shaped wings, varying from deep brown or black with yellow and reddish orange markings to faintly yellow transparent wings with faint blotches of colour, and with their slow very characteristic flight, are amongst the most conspicuous and familiar inhabitants found in the forest glades of South America. The left-hand member of this pair (7, *Melinaea paraiya*) belongs not to the Heliconiides but to the group (Ithomiides) illustrated by Fig. 5.

In pair E we have again on the right side (10, *Heliconius telesiphe*) a typical Heliconid butterfly, while on the left (9, *Colaenis telesiphe*) is a butterfly from the same region of South America, closely resembling its fellow in general appearance, but shown by the details of its structure to belong to

a totally different group of butterflies, the Nymphalidae.

It will be admitted that this striking resemblance in pairs of insects belonging to different groups is a very extraordinary fact. What is its meaning? It would appear that in a large proportion of such cases of mimicry we have to do with a special case of warning coloration—in which, however, the particular arrangement of colours constituting the warning livery is not confined to a single species but common to more than one. Thus in the Heliconiides we have a group of butterflies provided with a definite defensive equipment in the form of their evil-smelling blood, which makes them exceedingly distasteful to insect-eating birds. They have in general a characteristic appearance which serves to warn off insectivorous birds and other animals which have either individual or racial experience ("instinct"). In many pairs or groups of species this general resemblance is increased to the degree described as mimicry, the species being indistinguishable so far as external appearance goes unless they be examined in detail. We have already seen the advantage of warning coloration to a species possessing it, its enemies learning to associate its distinctive appearance with the particular objectionable feature that goes with it, and consequently after experience refraining from interfering with it. Now the advantage of more than one species possessing a distinctive warning coloration in common is that thereby the number of individuals possessing it in a given locality is rendered greater, and the experience, and consequently education, of the enemy is thus brought about in a shorter period of time. Or to look at

the matter from a different point of view, the number of individuals sacrificed to the education of the enemy is reduced in proportion by their being distributed amongst the greater number.

This type of mimicry, in which a particular scheme of warning coloration is common to the individuals of more than one species, is known as Müllerian mimicry, after its discoverer, the German-Brazilian naturalist Fritz Müller. Poulton has termed it Synaposematism.

In the cases so far considered the warning livery is justified by the presence of some defensive weapon such as a sting, or the possession of a disagreeable taste or smell. There also exists, however, another type in which there is no such defensive feature present but in which the scheme of coloration is a more or less accurate replica of that possessed by some other creature which does possess such a defensive arrangement. Here we have to do with what is sometimes called true mimicry or Batesian mimicry, after its discoverer Henry Walter Bates, who wrote that fascinating book, *A Naturalist on the River Amazon*—a description of his eight years' work as an entomologist upon the banks of that river.

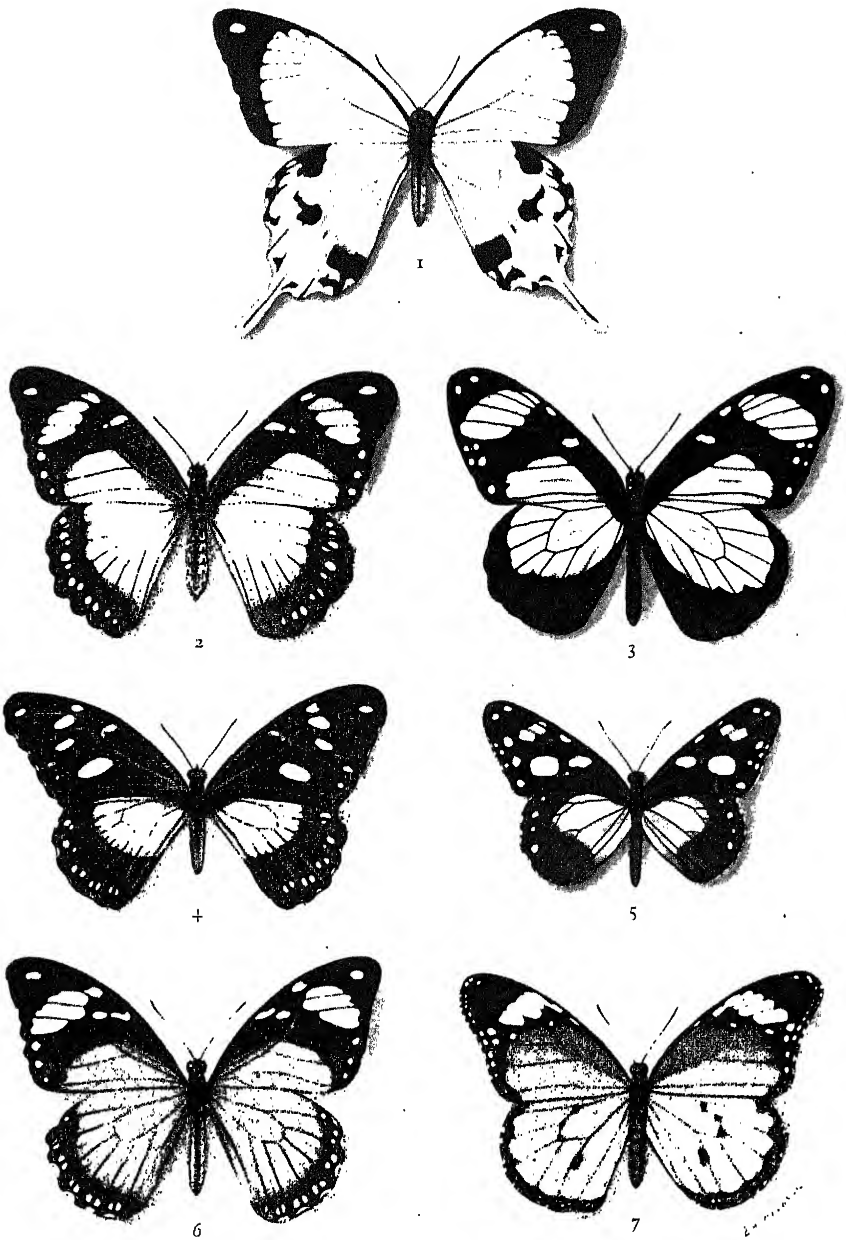
In Batesian mimicry the potential enemy is deluded into the belief that it has to do with a creature protected by some unpleasant characteristic, and as a consequence refrains from attack. Good examples are found in relation to the Heliconiides, distasteful butterflies with the distinctive scheme of warning coloration already alluded to on p. 171. If one makes a collection of Heliconiides in some particular locality one not infrequently finds amongst the numerous Heliconids a few

specimens which, when examined in detail, are discovered to belong to a family of edible butterflies — the Pieridae — the family to which our common white cabbage butterflies belong. Here then, amongst the crowd of Heliconids distasteful to insectivorous birds by their evil-flavoured blood, and readily recognizable by their warning colours, we have these Pierids masquerading in the colour pattern appropriate to their Heliconid companions and in this way escaping attack. Such is a typical case of Batesian mimicry.

The number of cases of mimicry now known in the animal kingdom is large, but our knowledge is very often insufficient as yet to enable us to say with certainty in a particular case whether it is to be regarded as Müllerian or Batesian. A very good example of the former, which may be grouped along with that of the Heliconiides already mentioned, occurs among the insects of Mashonaland.[1] Amongst the most conspicuous insects are the flower-frequenting beetles of the genus *Lycus*, sluggish in habit, possessing the power of exuding an evil-smelling fluid, and exceedingly distasteful to insectivorous birds. The various species have a very characteristic colour scheme—of reddish brown with a dark band at the hind end running across the wing cases close to their tips. This warning colour scheme is not restricted to the several species of *Lycus*: it is shared by a number of other species of beetles belonging to at least six different families, by Hymenoptera (wasps, ichneumon-flies, etc.) belonging to five different families, by various species of plant-bugs (Hemiptera), by certain moths (Lepidoptera), and by at least one species

[1] Marshall, *Trans. Entomological Society*, London, 1902, Plate XVIII.

Plate II.




MIMICRY IN FEMALE OF *PAPILIO DARDANUS*

1—*P. dardanus*, male; 2—*P. dardanus*, "hippocoon" type of female, mimicking 3—*Amauris niavius*; 4—*P. dardanus*, "cenea" type of female, mimicking 5—*Amauris echeria*; 6—*P. dardanus*, "trophonius" type of female, mimicking 7—*Limnas* (or *Danais*) *chrysippus*

of two-winged fly (Diptera). The greater number of this large assemblage of insects which share the Lycid scheme of coloration appear to be provided with defensive arrangements such as disagreeable taste or the possession of stings, but it is possible that a few of them possess no such defence, but are merely trading on the similarity to those that do, *i.e.* their mimicry is not Müllerian but Batesian.

Of Batesian mimicry quite admirable examples occur in our own country in the case of harmless Lepidoptera and Diptera (flies) which mimic stinging Hymenoptera such as hornets and bumble-bees.

A very common characteristic of mimicry is that it is most pronounced in the female sex, where, of course, it is of greater value to the race—the safety of the female being of greater moment than that of the errant and easily replaceable male. One of the most remarkable of all known cases of mimicry is that of the African butterfly *Papilio dardanus*, illustrated by Plate II. In this case the male, while showing a considerable amount of variation, is on the whole a quite ordinary-looking Swallow-tail butterfly (Plate II. Fig. 1). In a few isolated localities (Comoro, Madagascar, Mombasa, Abyssinia) the females are in general appearance just like the males—as is the general rule with Swallow-tail butterflies. In most localities, however, in which *Papilio dardanus* occurs one looks in vain for females bearing any close resemblance to the males, the females bearing the semblance of butterflies belonging to one or other of several different species. Thus in South Africa the females are of the three different types shown on the left side of Plate II. (Figs. 2, 4, 6), the commonest being that shown in Fig. 4, the least common that

shown in Fig. 6. The meaning of these extraordinary divergences from the normal Swallow-tail appearance is seen by inspecting the right-hand column of the plate, which represents three common species of local butterflies belonging to the family of the Danaides characterized, like the Heliconiides, by distastefulness. Each of these aberrant types of female is seen in fact to be a close mimic of the Danaid butterfly shown alongside it on the plate.

The figures shown do not exhaust the eccentricities of the female *Papilio dardanus.* In a band across Central Africa another type occurs which mimics a butterfly (*Planema poggei*) belonging to another distasteful group, the Acraeides. And at least four other types are already known.

As may be imagined, the first statements that these various types of butterfly were actually females of *Papilio dardanus* excited a good deal of scepticism : the story seemed altogether incredible. However, its truth is completely established. In the Cape district, for example, all three types of female occurring locally have been hatched out from a single batch of eggs.

What has been said so far in this chapter has had for its object to bring out the main general principles of the coloration of animals. It must not be imagined that the colouring of any one species is necessarily governed by a single one of the factors I have mentioned. On the contrary, we find very frequently that the colouring of an animal is a complicated affair, in which analysis shows us the workings of a number of different factors.

Thus if we watch a moving butterfly—well protected by the speed and elusive character of its flight—we very often see that it is brilliantly coloured, while the same butterfly at rest, with only the under sides of its wings visible, shows a beautiful obliterative colouring resembling its background—its effectiveness helped by psychological factors as shown by its preference for suitable backgrounds, or it may be by some peculiar habit, as in our common Grayling butterfly, by its leaning over so that the wings are almost flat upon the rocky surface on which it rests.

A particularly beautiful example is the Indian Leaf butterfly (*Kallima*). Here the butterfly in flight is a conspicuous object with its brilliant colouring. When, however, it settles in a bush it vanishes absolutely from sight. A careful search may lead to its discovery, and then the reason for its disappearance is at once obvious, for the resting butterfly is seen to mimic with the most extraordinary exactitude a dead leaf. The hind wings are drawn out into slender tails which, touching the stem, simulate the petiole or leaf-stalk. The front wings similarly imitate in outline the tip of the leaf. Along the centre of the two wings, on their under surface, runs a dark line simulating the midrib, and coming off at appropriate angles from this are other dark streaks representing the side ribs. One of the most astonishing features is that, just as no two individual dead leaves are exactly alike, so also with the butterflies. While each one is in appearance a dead leaf there are endless little differences in detail. Here or there may be a little dark blotch simulating exactly a growth of fungus: here or there an

apparent break in the continuity of the leaf which close examination shows to be a little transparent window where the scales are absent.

In discussing the adaptive coloration of animals I have for the sake of clearness mentioned the various factors separately, but as a matter of fact in nature we frequently find that the perfection of the general effect is due not to one of these factors but to the combined action of several. For example, in the photograph shown in Fig. 41, taken from Thayer's book, the "dazzle" markings, the blurred outline, and possibly a certain amount of counter-shading, all contribute towards the inconspicuousness of the woodcock chicks.

A single factor even may be effective in different ways. Take, for example, the "dazzle" pattern of dark and light stripes. In the case of the zebra this bold pattern serves in a faint light simply to destroy the continuity of the surface and outline, and in that way to delay or prevent recognition. In the South American heron (*Ardetta involucris*) or in the butterflies mentioned on p. 160 the striping is effective by its harmonizing exactly with the surrounding light and shade effects produced by the rushes or grass. The same effect is beautifully seen in certain vertically striped freshwater fishes which hover motionless among the reeds, such as the Angel fish[1] of South America, living specimens of which are sometimes to be seen in public aquariums.

The object of this chapter has been, by taking

[1] *Pterophyllum scalare.*

one particular type of animal characteristic which plays a great part in differentiating one species from another, to demonstrate how the detailed study of this characteristic brings out the fact that it is to a great extent adaptive—in other words, it

FIG. 41.—Young American woodcocks (*Philohela minor*). Photograph by E. G. Tabor. (From *Concealing-Coloration in the Animal Kingdom*, by Gerald H. Thayer.)

is of distinct utility to the particular animal in its particular environment.

I have taken the colouring of animals as the material for this demonstration on account of its superficial and comparatively simple character.

The internal organization of the body in the various types of animal is of course a matter of far greater complexity, and our knowledge is still far from complete, but yet in regard to this too it may be said with confidence that the continued advance in knowledge is building up a more and more convincing demonstration that as in the case of colour so also the other characteristics that mark off one species of an animal from another are in great part adaptive—of utilitarian value to the species, and that consequently their evolution, from small beginnings provided by variation, is fairly explicable by the action of natural selection.

In the next chapter I will proceed to the consideration of various auxiliary factors which have undoubtedly played a highly important part in rendering natural selection potent as an agent of evolutionary change. I will take first Darwin's favourite factor of " Sexual Selection ".

# CHAPTER XII

## SEXUAL SELECTION: EVOLUTIONARY FACTORS AUXILIARY OR ANCILLARY TO NATURAL SELECTION

THE principle of Sexual Selection, to which Darwin attached great potency as a factor in evolution but the importance of which has been belittled by subsequent writers, is in point of fact a subsidiary section of the Natural Selection principle as defined in this volume. The usual custom among writers on evolution has been to concentrate attention upon natural selection as affecting the individual animal. The evolutionary process, however, deals not merely with the isolated individual, it has to do with the succession of individuals that constitute the strain or race. It has to do not merely with adaptive features that facilitate the persistence of the individual but also with those that facilitate the perpetuating of the race. Sexual selection is in its essence natural selection applied to this latter type of character.

Individuals or strains possessing any characteristic tending to increase the number of their descendants above the normal will be favoured thereby, the proportion of individuals possessing that characteristic will thus become greater, and the characteristic itself will tend to become

intensified. On the other hand, a characteristic carrying with it the probability of producing less than the normal number of descendants will tend in the course of generations to bring about the elimination of strains of individuals handicapped by its presence, and as a result the elimination of the particular characteristic itself. In this way there will tend to be brought about evolutionary change in the direction of greater efficiency in the perpetuation of the race.

Many and varied characters are involved in this type of efficiency, and therefore explicable by the working of sexual selection, but amongst them we may distinguish two main types.

The first of these include characteristics that render their possessor more efficient in sexual conflicts. Such are found especially in the more highly evolved animals in which it is a very general rule that there exist more male individuals than are necessary for carrying on the race, and in which as a consequence there exists rivalry which finds its expression in conflicts for the possession of the females. In the evolution of weapons that make for success in these combats, such as the horns and antlers of male ungulates or the spurs of various male birds, it is unquestionable that sexual selection plays a great part.

And it has to be remembered that besides actual efficiency in conflict the *appearance* of efficiency will play its part. We can readily see how an immense pair of antlers in a stag will have a deterrent effect on younger rivals out of all proportion to its greater efficiency as a weapon in the actual conflict. It is probably this psychological effect which has been responsible for the evolution of such grotesquely

exaggerated weapons as the antlers of the extinct Irish deer (*Cervus giganteus*).

The second category includes features that are sexually attractive. It is obvious that individuals differ greatly in their degree of attractiveness to the opposite sex. It is obvious also that factors contributing to such attractiveness will contribute to propagative efficiency: individuals possessing them will have the probability of producing larger numbers of descendants than those without them, and as a consequence there will be a tendency for such features to become accentuated until their development reaches the stage of interfering with the general efficiency of the individual as a whole.

It is again obvious that the same factor which leads to the further development of features that are attractive to the opposite sex, will similarly tend to the elimination of features that are repellent to the opposite sex.

Sexual selection has not, any more than other types of natural selection, anything to do with first beginnings. Its rôle is to encourage and guide as it were the evolution of trivial little casual variations into characteristics of conspicuous moment in the life of the individual and the race. The raw material available for sexual selection will consist of the ordinary characters of the species, but more especially such as are associated with its reproductive activities.

As examples of the kinds of characteristics the understanding of whose evolutionary development is rendered easier by the theory of sexual selection we may choose a few from the second category above mentioned: (1) the beautiful plumage of

many male birds, (2) the songs of birds, and (3) the scent glands of certain insects.

## The Colours of Male Birds

The point was made in last chapter that the presence of brilliant colouring on the surface of an animal is liable to occur without its having any special biological significance in itself: it may be due to the presence of chemical substances or physical structure which gives rise to the sensation of colour, in an animal regarding it, purely by the way. It will be well to remind ourselves again that such colour may be what civilized man terms beautiful, without that beauty having in itself any significance whatever—our ideas of the beautiful being entirely a product of education and experience. And again as regards cases where the female of a brilliantly coloured male is of sombre and inconspicuous colouring that it is of advantage to the race that she should be inconspicuous when fulfilling her all-important function of incubating the eggs, and that consequently, if there is a natural tendency towards brilliant colouring, natural selection will exercise a powerful influence in keeping this in check in the case of the female.

What the upholder of sexual selection believes is that this factor has probably played an important part in working up casual colouring of the feathers into the gorgeous plumage seen in many male birds. Individual males showing a colour variation in a particular direction are rendered thereby more attractive, are more readily accepted by the female, and will consequently tend to leave larger numbers of descendants—imbued in turn with a similar

hereditary tendency towards this particular variation. In the case of birds in which the female is appreciative of brilliant colouring, such favouring of males a little more brilliantly coloured than the normal must necessarily, as I believe, lead to the evolutionary intensification of the brilliant colouring until its additional attractiveness comes to be counterbalanced by some accompanying disadvantage. Only the ignorant critic will suggest that the existence of such appreciation on the part of the female bird is pure assumption. No field naturalist who has watched the delightful courtship displays of their fine feathers by male birds in front of the female will have any doubt about the matter. Even among domesticated birds such displays are familiar in the case of peacocks. Apart from such evidence we have the fact that various birds do actually appreciate brilliant colouring demonstrated by numerous cases in which birds (*e.g.* Bower birds) are known to decorate their nests or their surroundings with brilliantly coloured objects such as iridescent insect wings, coloured stones or shells.

An analogous case to that afforded by the colour of birds is that of spiders, the wonderful colours and forms of which are most striking to the naturalist working in tropical regions. Spiders differ from the majority of arthropods in having very highly developed eyes, which, like the eyes of vertebrates, afford a detailed image of the object that is being looked at. And it is well known that the courtship of spiders is characterized by the male performing the most extraordinary dances and poses in front of the female so as to display his physical charms to her in the most effective way.

### Vocal Attractions

Whereas the males of some animals specialize in brilliant colour, or complex pattern, or striking form, others specialize in the production of sounds attractive to the other sex. That there is such attraction is unquestionable: a female cat will struggle to reach him when she hears the call of the male; a female canary will favour the best singer; the female cricket or cicada is attracted by the note of the male. In all such cases it is unquestionable that the female appreciates the vocal powers of the other sex, and it is a necessary consequence of this fact that the voice will tend to evolve towards greater perfection.

### Aromatic Attractions

In a large number of terrestrial animals special scents are produced which attract the other sex. These are particularly well marked in mammals and in various insects. Insect collectors use as one of their stock methods for obtaining the males of certain moths the imprisonment of the female in a gauze cage through which the air circulates freely. The males are attracted from long distances by the scent produced from certain areas of the body surface. It is clear that a female in which this scent-production is more than usually potent and attractive will have a distinct advantage as regards handing on her hereditary tendency in this direction, in comparison with another female in which the power of producing the attractive scent is absent or feebly developed. Consequently the action of sexual selection would be to build up and

develop any feeble beginnings of this power occurring as a chance variation in a species previously without it.

I have so far endeavoured to make clear :

(1) That natural selection, or survival of the fittest, or the elimination of the less fit, is a process actually at work in Nature, and that it must of necessity bring about evolutionary change in the way of developing features which are of use in making and keeping the organism intimately adapted to the circumstances of its environment; (2) that the study in detail of features that distinguish animals from one another, such as their colouring—to take the particular example that I have made use of, shows that a large proportion of such features are of direct adaptive utility to the animal and consequently come within the scope of natural selection as an evolutionary factor; and (3) that what Darwin termed sexual selection plays an important part in this process in relation to certain types of character.

### Correlation

Natural selection is concerned primarily with features of direct utility to the animal, but through the workings of the principle known as correlation such directly useful developments are apt to bring in their train others that are not in themselves of utility. In this way natural selection may become indirectly responsible for features that are not adaptive.

Already in the early days of the science students were struck by the appearance of strange phenomena indicating a mysterious correlation between different features of the animal body. Thus Darwin mentions (*Origin*, chap. i.) that amongst pigeons length of head and size of foot are apt to go together, or again that amongst male cats the (rare) occurrence of blue eyes is apt to be associated with deafness.

While this phenomenon of correlation is as yet by no means fully understood, still our knowledge of it has advanced far since Darwin's day. It has become clear in the first place that we have to do with two fundamentally different types of correlation, which I will designate by the term *primary or gametic correlation* and *secondary or physiological correlation.*

The first of these is exemplified most clearly by certain results of the beautiful investigations carried out in the zoological laboratory of Columbia University by Morgan and his school. These investigations were carried out on a species of *Drosophila*—a small greyish-brown two-winged fly with red eyes, which deposits its eggs on fermenting fruit and can be reared in large numbers with great facility.

In studying the inheritance of various abnormal features which turned up sporadically in these flies it was found that particular peculiarities tended to be inherited together. This binding together of features into heritable groups is commonly termed " linkage ". Out of forty-seven specially important heritable characters mentioned by Morgan, and which we may designate by the numbers 1 to 47, numbers 1-15 were found to be linked together; 16-28 were similarly linked: so also with 29-44; and with 45-47. In other words there were

four groups—three large and one small. A further point to notice is that the first group of characters is linked with *sex*, these characters occurring consistently in one form in the male, in the other form in the female.

Now these facts, ascertained by practical breeding experiments, are found to agree precisely with the facts of nuclear constitution in *Drosophila*, for the haploid set of chromosomes are four in number, three large and one small and dot-like. Further, one of the large chromosomes is the sex chromosome X in the female, Y in the male (p. 106). And we are therefore fully justified in concluding that such correlation of characters is brought about through the hereditary substance representing them being located in the same chromosome.

There occur, however, other cases of correlation regarding which this type of explanation is not open to us. For example, a change (A) in one of the important glands of the body may bring about a characteristic change in the internal medium, and this in turn cause modification (B) in other characters of the body. In such a case the changes grouped under B show correlation with one another and with the change A, but the correlation is brought about not by proximity of the corresponding parts of the heredity-bearing substance in the gamete but by the physiological activity of the individual body. Such correlation is what I have termed secondary or physiological correlation.

This type of correlation is well exemplified by characters associated with the sex of the individual. It is now realized that in the higher animals the genital gland—ovary or testis—while carrying out its primary function of producing the gametes or

reproductive cells, at the same time discharges into the blood obscure substances which have an important influence not merely upon the health and living activities of the body but also upon its growth. Among the vertebrates many of the features characteristic of the body in the two sexes are primarily due to the influence of such substances. Such, for example, are the antlers of male deer: these fail to develop in individuals from which the genital glands have been removed.

It is not merely the sex-glands which serve to link together other developments of the body. The same applies to the activities of other glands. If, for example, the ductless gland known as the thyroid fails to function normally in a child, the bones do not develop to full length, and in fact the whole development, mental and physical, is retarded, so that at the age of thirty the whole condition is childish.

So also with other ductless glands, and probably indeed with every portion of the living body: so long as life lasts in the particular organ or tissue there pass from it into the circulating blood, and so into the general fluid of the body or internal medium, the special waste products of its living activity; and any departure from its normal behaviour in discharging these substances is liable to produce far-reaching effects upon the individual.

The general conclusion to which we are drawn may be shortly stated thus: that a variation involving change in the living activities of one part of the body, more especially such a part as a ductless gland, necessarily carries with it other changes that are linked to it by physiological correlation. It is clear that in this way the field covered by the action

of natural selection or sexual selection becomes greatly widened, and that evolutionary changes may be indirectly due to their action although it is quite impossible to trace any connexion of a direct kind.

### Evolution a Function of Environmental Change

A difficulty often suggested as being in the way of the Darwinian explanation of the evolution of adaptive arrangements is this: Is it conceivable—it is asked—that evolutionary progress towards more and more perfect adaptation should go on indefinitely? Must not such progress come comparatively soon to an end through the whole animal population reaching a state of practically perfect adaptation to the world in which it lives?

Here we come into touch with a failure on the part of evolutionary writers—as general as it is remarkable—to realize to how great an extent evolutionary change is dependent upon environmental change. The reciprocal relations between an animal and its environment are as a matter of fact subject to constant change. On the one hand, the environment itself changes. Changes of climate take place. The conformation of the land changes: valleys are carved out, hills are removed by erosion, swamps become dry, dry land becomes swamp, and so on. And along with, or independently of, such changes come changes in flora and fauna—the whole complex of changes in a given area constituting change in the environmental conditions of the various members of the animal population.

In other cases the active factor of change is the animal itself, through change of habits. It gradually alters its food. From being terrestrial it becomes arboreal: from being arboreal it becomes terrestrial—like the Pampa woodpecker (*Colaptes agricola*), which has taken to feeding on the Termite nests of the treeless Pampa. It leaves the swamp and takes to the dry land. It migrates from the sea into fresh water. Or it develops any other of countless possible changes in its habits.

In either type of case there is brought about change in the reciprocal relations of animal and environment. In many cases changes in the environment itself are apt to be disastrous; for example, a sudden irruption of the sea into fresh-water swamps. But if the change is very gradual, as such changes in Nature usually are, the gradually changing standard of fitness will be liable to carry with it the gradually changing animals, through the continued selection of those individuals whose variations make them on the whole more fit to survive under the changed conditions.

In my opinion it is probable that this step-by-step and side-by-side progress of organism and its environmental relations is to be regarded as one of the great general principles of evolution. In many cases the linkage of the evolving organism may be particularly direct with some comparatively minute factor in the environment; such, for example, as some accompanying species of animal to which it is linked by the relations of parasite to host, or of mimic to model.

I might summarize my view of the matter in a sentence, namely, that the rôle of natural selection is to keep the organism in direct adaptation to its

environmental relations, so that as these latter change the organism changes with them.

If this view is a sound one it is of great importance in relation to an argument brought against the evolutionary potency of the selection of small variations adduced by some experimental breeders. The Dutch botanist De Vries, for example, while admitting that the selection of such small variations will produce evolutionary change, minimizes the importance of this, for, he says, as soon as selection ceases reversion will take place to the original form. The actual fact, as I believe, is that in wild nature selection *never* ceases. It is actively at work the whole time, keeping the species in close adaptive relation to its slowly changing environment. Consequently, the fact that varieties produced by artificial selection slip back to the ancestral condition as soon as the selection stops has simply no bearing upon the actual evolutionary process under natural conditions.

## Isolation

A difficulty that presented itself to some of the earliest critics of Darwinism is the liability of favourable variations, present in relatively few individuals, to be swamped through interbreeding with individuals that do not possess the particular variation. This difficulty appears less formidable than it did in Darwin's day. Mendelian research has shown us how particular individual peculiarities are liable to be handed on to larger and larger numbers of descendants in apparently undiluted intensity: and there is further the action of heredity

in accumulating or intensifying the tendency of variation to keep on along a definite line.

Nevertheless the danger of favourable variations being swamped by intercrossing must still be admitted to be real. The great auxiliary factor which acts as a safeguard against this is the **isolation** of the favourably varying individuals. In the evolution of domesticated animals this isolation is brought about by the breeder, who gets rid of or sterilizes the individuals whose variations are not in his eyes "favourable". In the case of wild animals isolation is brought about in many ways. The simplest is mere geographical isolation, where part of a species becomes isolated by geographical barriers. In the case of a species spread over a wide area, its dying out in an intervening region may lead to the isolation of a section of the species from the main body and so enable it to go on evolving independently: or sections of the species may become isolated on islands or other districts enclosed within efficient barriers.

An excellent example of such geographical isolation on a miniature scale is disclosed by Gulick's fifteen years of investigation of the snails of the Sandwich or Hawaiian Islands. In these islands are to be found a group of snails known as the Achatinellidae. Adapted as they are to life in the damp shady forests of the valleys, open country with its glare and drought forms an almost insuperable barrier to their wanderings. A still further degree of isolation is brought about in many cases by the species being strictly arboreal in its habits. The restriction of free intercourse brought about by these isolating factors has resulted in extraordinarily active evolutionary change, *e.g.* in the island of

Oahu eight genera of Achatinellidae have diverged into a multitude of different types, each restricted to a small patch of forest. And further, as the observer passes along the series of valleys he finds that each valley differs slightly in its snail population from its immediate neighbour, so that the divergence between more distant parts of the island bears a rough proportion to the distance between them.

It is obvious of course that physiological factors have much to do even with ordinary topographical isolation, for the efficiency of barriers depends upon the inability of the living animal to pass them. But there are other barriers, and these probably of even greater evolutionary importance, which are in themselves entirely physiological in their nature. All evolution is necessarily dependent on hereditary transmission, and in the vast majority of animals this involves two parents. Change in breeding habits, for example a change of breeding season accompanying a particular kind of variation, will obviously form an exceedingly effective barrier, isolating individuals showing this kind of variation from others which do not.

Again, the reproductive function is known to be one of the most delicate in the body, and to be liable to interference by all kinds of obscure psychical and other physiological conditions. A very slight divergence may be sufficient to destroy sexual attraction between the divergent individuals on the one hand and those on the other hand which do not show the particular divergence, and this again will constitute an effective physiological barrier isolating the divergent individuals from the rest of the species. Or conversely similarly varying

individuals, possessed of special sexual attraction for one another, will thereby be isolated to a certain extent from other individuals by an impalpable but it may be very efficient barrier so far as reproduction is concerned.

Other physiological barriers of a more obvious kind are afforded by changes in ordinary habits, such as concentration in a particular neighbourhood where food is abundant, or migration into a different environment. Particularly well marked are cases where the animal takes up an association with some particular kind of plant or animal. Such an association, best marked in the case of parasites, becomes an effective means of isolation.

However brought about, it is clear that all such forms of isolation must play a part of the very highest importance in facilitating, or even rendering possible, the evolutionary action of Natural Selection.

## CHAPTER XIII

### COMMUNAL EVOLUTION

THE process of evolution finds expression not merely in the structure of the individual but also in those associations of individuals which we call communities. The more important general principles which govern communal evolution are rendered clear by the study of cell-communities, in which we can see innumerable steps in the evolutionary process, between the primitive isolated cell-individual belonging to the group Protozoa and those enormously complicated cell-communities that constitute the bodies of the higher animals.

In the case of the Protozoa the zygote, the cell-individual formed by the union of the gametes, eventually divides by fission into two or more individuals like itself, and these usually separate and lead their own independent lives. In a few cases, however, the cell-individuals do not separate but remain attached together forming a primitive community. In the simplest type of such a cell-community we see that (1) the community is small, composed of relatively few cell-individuals; (2) the cell-individuals are alike, unspecialized; and (3) they are only loosely attached together.

On the other hand, when we examine the relatively highly evolved community that forms the

body of one of the higher animals we find a striking contrast.

(1) The community is relatively enormous, composed of myriads of cell-individuals.

(2) These individuals differ greatly from one another: they are highly specialized for the performance of the various communal functions. Thus the superficial layer of cells is specialized in one way and another to form a protective skin. Certain tracts of cells in the interior are specialized to form a rigid skeleton to support the soft and yielding mass of living substance: other cells are modified to form contractile muscles by which the parts of the skeleton can be moved on one another, and so movement of the body as a whole brought about. A layer of cells tucked inwards from the surface forms a tube lined by cells specialized for the mastication, digestion, and absorption of food. Other tubular arrangements of cells specialize in the excretion of the poisonous waste materials constantly being produced by the living activities of the cells of the community.

(3) The members of the cell community are linked together by an exceedingly complex organization so as to ensure their harmonious co-operation in the activities of the whole individual.

In this organization the main parts are played by the nervous system and the blood system. The former serves to gain information through its sensory cells regarding what is going on in the world outside, to consider the impressions so received, to activate and control the appropriate reactions on the part of the individual, and to keep the different parts of the individual linked together. This latter function is helped by the elaborate transport system

constituted by the blood contained in its tubular channels passing from and to all parts of the body. By means of the central pumping station, the heart, the blood is caused to circulate all through the system of blood vessels. It carries with it supplies of oxygen, in the special little vehicles called red corpuscles, while it brings back from the crowded cell-community carbon dioxide and other waste products of its living activity. It also serves to distribute throughout the body the heat formed by the oxidation processes in the cells, and so keep the whole cell-community, even its surface layers, at nearly the optimum temperature. The circulation also brings the important advantage that it renders possible the concentration of particular functions, such as the taking in of oxygen from the surrounding medium, the extraction of waste materials passed into the circulating blood by the various members of the cell-community, the absorption of the products of food-digestion, and so on, in localized spots in the body, thus allowing parts of the cell-community to become highly specialized for one or other of these particular functions. A large contingent of the cells, less highly specialized than the others, retain the primitive amoeba-like form, creeping about in the fluid internal medium of the body—the complicated watery solution or lymph which bathes the surface of all the cells of the body, and a special part of which forms the circulating blood. These mobile cells, while functioning as scavengers to get rid of the remains of dead cells or other objectionable materials, also form a mobile defence force to attack and destroy microbes which have pierced the outer defences of the body formed by the skin.

While the general cells of the body have become more efficient for playing their part in the cell-community by becoming highly specialized, they have paid a price for this, in that they have lost the ancient power of undergoing the process of syngamy which in the Protozoa is associated with the continuation of living existence. Only at one or two, or sometimes more, points in the body do we find a patch of cells which retain their ancient power. These constitute the gonad—the mass of reproductive cells.

When we turn from such cell-communities to communities in the ordinary sense of the word—associations of completely developed individuals—we see the working of the same general principles. Among the lower groups of animals we find that the community consists of a family or clan of individuals, all descendants of a common ancestor and in more or less complete organic continuity with one another. The individuals are fixed in relation to one another, and the community as a whole is usually attached to some solid object, though in a few cases it floats freely in the water.

Fig. 42 illustrates a small piece of such a community of *Obelia*, a lowly organized animal belonging to the Coelenterata, a group or phylum which zoologists place near the bottom of the scale of animal life above the Protozoa. The community is composed of simple little hydroid polyps, each with a large trumpet-shaped mouth (*o.c.*) surrounded by a circle of slender tentacles, and each in continuity with the other members of the community through a strand of living substance. The members of the community are not all alike. The majority are ordinary polyps such as has been mentioned,

but here and there we find a quite different looking individual (*bl.*). This is devoid of tentacles, devoid of mouth, and is therefore quite unable to feed. It is an individual devoted entirely to reproductive purposes. From its side it buds off numerous little umbrella-shaped individuals (*M*) looking quite unlike any of the other members of the community.

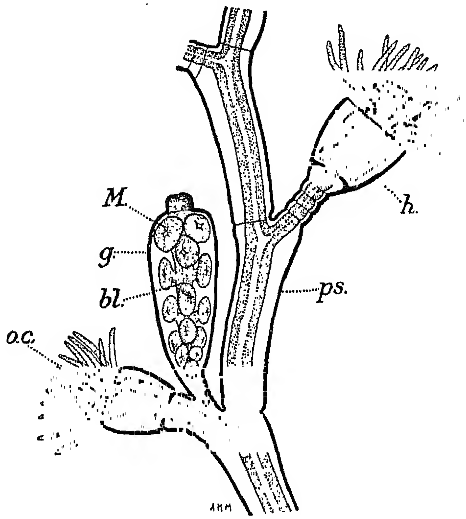



FIG. 42.—Part of community of *Obelia*. (From Graham Kerr, *Zoology for Medical Students*.) *bl.*, blastostyle; *g*, gonotheca—a vase-like receptacle enclosing and protecting the blastostyle; *h*, hydrotheca—a cup-like receptacle enclosing and protecting an ordinary hydroid polyp; *M*, young medusa budding off from blastostyle; *o.c.*, mouth of polyp; *ps.*, horny covering protecting communal stem.

These eventually break off and desert the community, swimming away through the water as minute Medusae or jelly-fish. These very highly specialized errant individuals have for their function the production of gametes and, through them, of new communities: they in fact are the sexual individuals of the original community.

In such communities as that of *Obelia* the

ordinary members of the community form a continuous whole, never having become separate, but remaining linked together by continuous living substance. In the case of the more highly evolved types of animal, on the other hand, the bodies of the individuals are sharply demarcated, and when they live in communities the individuals are linked together not by continuity of their material substance but by the intangible organization formed by social customs. Various stages in the evolution of such colonies are seen amongst the insects—particularly among the bees and wasps, the ants, and the termites or so-called white ants.

Amongst the various species of termites we find innumerable stages of social evolution, from small communities of a few unspecialized individuals up to communities of several millions, showing a very high degree of specialization. The typical termite is devoid of the light-proof coat of pigment which is the usual possession of the more complex animals, and the snowy-white fatty tissue, which forms a packing round the internal organs of all insects, consequently shows distinctly through the transparent skin, and this fact has given rise to the misleading popular name "white ants". Physiologically related to the same characteristic is the habit of termites to live in complete seclusion from daylight, within nests built of particles of soil, or masticated and partially digested wood, firmly cemented together. Where, as is often the case in South American termites, an annex to the main nest is built in a tree a light-proof tunnel is built up the side of the trunk by which the termites can move up or down without exposing themselves to the light. Large termite nests may form "ant-

hills" as much as 20 feet in height, within whose light-proof fastness lives the termite community with, it may be, domesticated animals of varied kinds, such as extraordinary beetles, found nowhere else, in which the huge and greatly modified abdomen grows out into bizarre projections from which exude food material that is licked off by the termite proprietors. In some of the Old World species of termite communal gardens exist and are carefully tended, in which are cultivated the mycelium of certain mushrooms, treated in some unknown fashion so as to produce little round tumours which form nourishing food. These fungus gardens[1] are usually crowded with young termites which subsist upon this fungal food, as do also the king and queen, but not the workers or soldiers.

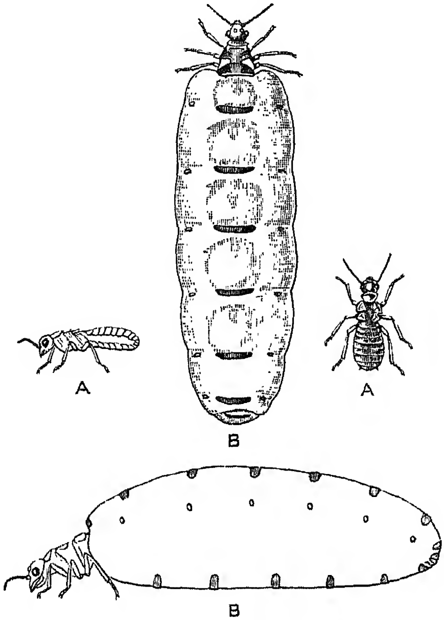



FIG. 43.—Sexual individuals of *Termes malayanus*. (From Sharp, *Cambridge Natural History*.) A, male ("king"); B, female ("queen").

In a typical termite community there are found five different castes of individuals. First come the father and mother of the community, the

[1] It is an interesting fact that in the New World very similar mushroom gardens are run by true ants—the large black leaf-cutting ants (Attidae) that are so conspicuous in the warmer parts of the American continent.

so-called king and queen—deeply coloured, with large well-developed eyes, and with the stumps of cast-off wings—features, all of them, correlated with the fact that these two individuals alone have lived for a brief few hours in the day-lit world outside. In the early days of the community, and for a more or less prolonged period, these two are the only sexually mature individuals. In some species the queen is enormously enlarged (Fig. 43, B) owing to the immense increase in the size of the ovaries correlated with the fact that she goes on producing eggs steadily at a rate of sometimes as much as a thousand every day for a period which may apparently be as long as ten years. The royal pair are carefully fed and tended, and commonly have a special chamber right in the centre of the nest. In spite of every precaution accidents may happen, and as a provision against these there is commonly a reserve supply of potentially sexual individuals which when the need arises may, by some mode of treatment quite unknown to us, be caused to become sexually mature. There may be two different types of these reserve individuals, some with a distinct amount of pigment and with distinct, though reduced and useless, wings, and others which have hardly any pigment and are completely wingless.

Apart from these actual or potentially reproductive individuals is the ordinary mass of the community, consisting of wingless unpigmented individuals which can be recognized as male or female in type, but in which the reproductive apparatus is entirely degenerate and functionless. Amongst them can be recognized two main classes, although each is in some species further subdivided, (1) the

ordinary citizens or workers, and (2) peculiar individuals known as "soldiers", whose function in the community is not always very obvious, provided with greatly swelled heads and often with formidable-looking weapons in the form of huge jaws (Fig. 44). In some types of "soldier" (Fig.

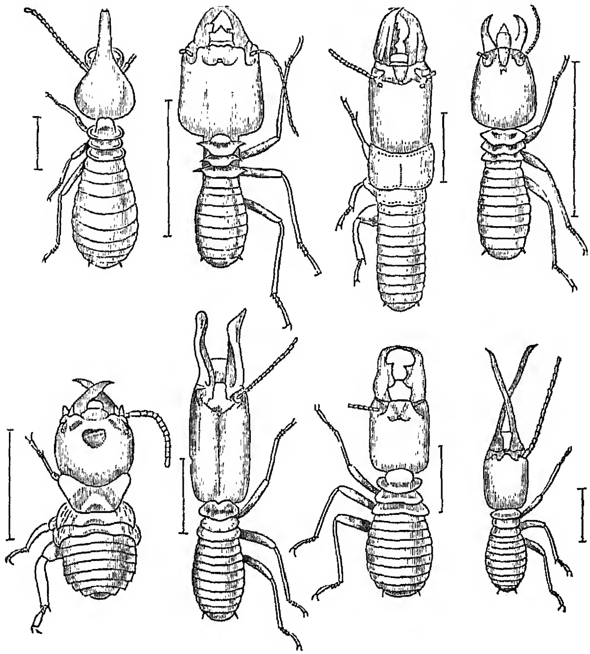


FIG. 44.—Soldiers of eight different species of termite. (From Sharp, *Cambridge Natural History*; after Hagen.)

44, top left-hand figure) the head is prolonged forwards into a tubular snout, at the tip of which is an opening through which a birdlime-like secretion can be ejected which effectively pinions an obstreperous opponent.

Besides the grown-up citizens of the community there are the innumerable young in the fungus-garden nurseries. From these grow up recruits for

the various sections of the community. Those that are young " kings " and " queens ", dark coloured and provided with fully-developed wings, when a day comes on which the weather conditions are suitable, creep out of the nest—untold millions covering the ground on a particularly favourable day and providing food to repletion for insect eaters of all kinds—and eventually, such as survive, take to flight in pairs. A successful couple alight at a suitable spot, excavate for themselves a burrow in the earth, disappear into it, drop off their wings, and lay the foundation for a new community.

As has been mentioned the termite communities illustrate many different grades of social evolution, and the point should not be missed that Nils Holmgren, one of the chief investigators of termites, finds that while advance in social organization is accompanied, as we might expect, by advance in the nervous organization of the individual, it is also accompanied by a process of degeneration as regards its characteristics in general.

An important point that should be clearly grasped in relation to communal evolution is that the entire community evolves *as a community*. In the cellular community constituting the body of one of the more complex animals the evolutionary progress, from generation to generation, of the cell-individuals is an inseparable part of the evolution of the whole. This is obvious if one considers that there is no direct descent from the specialized cells—muscle cells, or nerve cells, or gland cells, or any other type of specialized cells—of one generation to the corresponding cells of the next. As has already been indicated these specialized cells are sterile, the function of producing the next generation being

restricted entirely to special members of the cell-community, those constituting the gonad.

Precisely the same principle holds with the more highly-developed types of community in the ordinary sense, such as the more complex termite communities. Here again the ordinary specialized citizens of the community are sterile: their evolution, as time goes on, is simply a part of the evolution of the colony as a whole. Increased specialization of the individuals for their special communal functions means increased efficiency of the colony as a whole, and this involves a better chance of long life and prosperity, with its accompanying giving off of incipient new communities.

It is a striking sight to look out across a broad plain crowded with termite hills, and one cannot but reflect on the tremendous struggle for existence that there must be in view of the enormous numbers of young communities seeking the opportunity of establishing themselves, a struggle ensuring the crushing out of existence of communities that have lost their communal efficiency and their replacement by others whose efficiency in the struggle is unimpaired.

## BOOK FOR FURTHER STUDY

WHEELER. *Social Life among the Insects.*

# CHAPTER XIV

## EVOLUTION AND MAN

WHAT do we know regarding the evolutionary past and probable future of Man? There we have one of the most absorbingly interesting questions connected with evolution. The scrappiness of the answer is apt to be disappointing, but we must bear in mind that such scrappiness applies to all evolutionary knowledge. What we actually know is restricted to mere fragments which, fascinatingly interesting as they are, seem yet almost ridiculous in comparison with what remains unknown.

It is of course clear that the civilized man of to-day has evolved from savage ancestors. None of us doubts the fact that if we could trace our ancestry backwards for a few thousand years we should arrive at people destitute of everything that constitutes what we call civilization, and leading a primitive nomadic hunting existence like that of the lowest savages of to-day. To one who has lived the life of such savages it is of extraordinary interest to notice every now and then the working of ancient ancestral ideas amongst our ordinary feelings: the instinctive dislike of the darkness of night—the time when the savage is in continuous anxiety about the dangers of the unseen around him; the cheery feeling as one sits by the flickering fire—in the life

of the savage the damping down of the fire is one of the first precautions against impending danger, while the allowing it to blaze up means freedom from anxiety as to danger from enemies; the enjoyment of the sound of the rippling streamlet—the sound betokening freedom from the sufferings of drought; the pleasant sensations of green and blue, the colours of the forest and the sky—the unpleasantness of darkness and red with their suggestions of tempest and fire.

Archaeologists have been able to piece together much information regarding these savage ancestors of civilized man from stone implements and relics left behind by them, while we can deduce much more from the study of existing savages in a corresponding stage of evolution. However, we are concerned here with still earlier phases, before our ancestors had established their claim to the adjective human. In attempting to glean information as to these pre-human beings we should naturally turn to our usual three sources of evolutionary information, and in doing so we find, in the first place, that comparative anatomy shows man to be undoubtedly a member of the group Primates, to which apes, monkeys, and lemurs belong—all the members of that group, including man, being linked together by close community of structure. In the early days of Darwinism bitter controversy was raised on the realization of this fact by persons who disliked the idea of having poor relations in the form of apes and monkeys, but these controversies have long since died down, except among the ignorant, and have given place to complete agreement among those competent to judge that the inclusion of man in the same zoological group

as apes and monkeys is unavoidable. This conclusion, resting on the facts of comparative anatomy, is clinched by the evidence of the serum test (p. 50), which brings out a close blood relationship between man and the anthropoid apes. Corroboration also comes from the facts of pathology, the anthropoid apes being susceptible to diseases of man to which other mammals are immune.

The reader without training in comparative anatomy will easily convince himself of the truth of this conclusion by turning over the pages of an illustrated work on that subject, or, still better, by going to a zoological museum and comparing the skeleton of a man with that of other primates. In the latter case he will see how the soft parts of the body are supported by a skeletal framework consisting of an identical set of bony pieces, the differences being merely slight differences in the size and shape of the individual pieces.

The general purport of the facts of comparative anatomy is to show that the nearest blood-relations of man are the anthropoid apes. It is not, of course, suggested that man has evolved out of any one of the four types of existing anthropoid ape—chimpanzee, gorilla, orang-utan, or gibbon: to do so would be to flout what is probably to be regarded as a correct general principle of evolutionary theory, namely, that *no* evolutionary ancestor of existing animals is to be found persisting unchanged upon the earth to-day. The conclusion rather is that the four existing types of anthropoid, together with man, are the evolutionary descendants of a common ancestral type, but at the same time we are safe in believing that the anthropoids have diverged far less from the common ancestor than

has man. Each of the four types of anthropoid has developed little peculiarities of its own, but, on the whole, we may say that the chimpanzee and gorilla are closest to man and the gibbons farthest removed from him.

Passing downwards from the anthropoids we come to the catarrhine or Old World monkeys, the platyrrhine or New World monkeys, and the lemurs, more especially the quaint little Tarsier (*Tarsius spectrum*) of the Malayan Archipelago, each of these groups suggesting a step farther away in evolution from man, though each in turn possessing special peculiarities indicative of its having undergone divergent evolution along its own path since the days of the ancestor it had in common with human beings.

It must not be supposed that the members of the group Primates, whether man himself or any of the others, have reached an outstandingly high stage in the general structure of their bodies. On the contrary, they are surpassed by many other vertebrates. A horse, or a cat, or a bird, might quite fairly be regarded as representing a higher grade of evolution in its general structure than man. Man owes, in fact, his predominant position not to the high degree of development in his body as a whole, but rather to the high development, in structure and function, of one particular part of the body, namely, the brain.

Passing beyond the limits of the group Primates, we find that the existing mammals which seem most closely akin to the lower primates are the arboreal shrews of the genus *Tupaia*, found in the forests of Malaya.

The contributions of embryology to our know-

ledge of human evolution are not so much informative as simply corroborative of what might be expected on general grounds. The first stage of the human individual is the single cell or zygote representing the Protozoan phase. Later on, when the typical vertebrate characteristics have developed, we find the sides of the neck pierced by the typical gill-clefts used by the fish for breathing; the great arteries are in the form of typical aortic arches for the conveyance of blood to those clefts, although it is no longer required there as it is in the fish; the skeleton is at first a simple notochord, and thereafter, for a long period after it has assumed the general arrangements of the adult skeleton, it is composed of the unossified cartilage characteristic of the lowest fishes; the body ends in a distinct tail, and is for a time before birth covered with a coat of fur. In these and in many other details of the various organs, the human embryo passes through phases entirely in agreement with the past history of man postulated by the evolution theory. And this agreement is continued in postnatal development: the infant in his creeping movements, his power of supporting himself by hanging on with his hands, his feeble mentality which gradually evolves into the mind of man, continues to testify to his evolutionary past.

Palaeontological knowledge regarding man's past history is still of the most fragmentary kind. Each additional scrap becomes the subject of a voluminous literature and the basis of an edifice of speculation out of all proportion to the foundation upon which it rests, and not infrequently constructed in complete defiance of the accepted canons of morpho-

logical argument. No doubt this is quite understandable in view of the intense interest of the subject, but the serious student of evolution has to step very warily when he enters this field.

The oldest remains of man so far obtained are usually ascribed to the early Pleistocene period. We are therefore justified in believing that man existed as early as that period, but how much earlier he existed we do not in the least know. We may take it as fairly certain that primitive man, living by his wits, in small parties and not in large communities, was not likely to have his remains engulfed in large numbers under conditions favourable for fossilization, and that the palaeontological record of his history would be in consequence of a particularly incomplete kind. It is therefore quite unjustifiable to base upon the fact that we have not hitherto obtained fossil men of earlier than Pleistocene age the conclusion that he had not come into existence before that time. On the contrary, we should rather be justified in taking the discovery of a human fossil of Pleistocene age as indicating that by that time man had become an abundant type of creature, and that therefore his first appearance must have been long anterior to that period.

Still less is it justifiable to suggest a probable date for man's appearance on the earth. Statements of this kind, involving periods of time reckoned in hundreds of thousands, or millions, of years, are frequently made, but, like other attempts at the numerical expression of evolutionary time, they are not to be regarded as of scientific value.

The palaeontological data so far known bearing

upon human evolution may be summarized shortly as follows. The earliest anthropoid ape known up to the present is the Egyptian *Propliopithecus* of Oligocene age. During Miocene times anthropoid apes had on the continent of Asia diverged into numerous types, some of them pointing decidedly in the direction of man. From deposits in Java, most usually regarded as of early Pleistocene age, comes an undoubtedly human thigh bone, and a skull which most anatomists admit to be human, although so ape-like that some regard it as belonging actually to an ape. However, casts of the skull cavity show that the brain, although very small, was distinctly larger than that of apes, and further, that it possessed those special developments of the temporal region which are known in the case of the human brain to be concerned with the faculty of speech. In recognition of its mixture of apish and human characteristics this creature has been placed by its discoverer, Dubois, in a genus by itself and called *Pithecanthropus*.

The next stage made known to us so far by palaeontology is the Piltdown man—*Eoanthropus*, represented by fragments of a skull obtained from gravel of probably early Pleistocene age in the county of Sussex, with a brain relatively larger than that of *Pithecanthropus*, but with a lower jaw so like that of an ape that some competent authorities have still doubts as to whether it would not be justifiable to regard it as being definitely an ape's jaw which, separated from its own skull, had by an extraordinary coincidence come into close juxtaposition with a human cranium that did not by rights belong to it.

In addition to *Pithecanthropus* and *Eoanthropus*

three other species of fossil men are commonly recognized, which are included in the genus *Homo* along with modern man (*H. sapiens*), under the names *Homo heidelbergensis*, *H. neanderthalensis*, and *H. rhodesiensis*. Of these three species the second is best known, owing to the relatively large numbers of skeletal fragments that have been obtained belonging to it, and Elliot Smith [1] gives a graphic and clear-cut picture of the uncouth and repellent Neanderthal man. "His short, thick-set, and coarsely built body was carried in a half-stooping slouch upon short, powerful, and half-flexed legs of peculiarly ungraceful form. His thick neck sloped forward from the broad shoulders to support the massive, flattened head, which protruded forward, so as to form an unbroken curve of neck and back in place of the alternation of curves, which is one of the graces of the truly erect *Homo sapiens*. The heavy overhanging eyebrow and retreating forehead, the great coarse face with its large eye-sockets, broad nose, and receding chin, combined to complete the picture of unattractiveness, which it is more probable than not was still further emphasized by a shaggy covering of hair over most of the body. The arms were relatively short, and the exceptionally large hands lacked the delicacy and the nicely balanced co-operation of thumb and fingers which is regarded as one of the most distinctive of human characteristics."

The other two species of fossil men are much less well-known. *H. heidelbergensis* is represented by a single jaw found in the Mauer sands—of geological age probably about the commencement of

[1] *Proc. Brit. Acad.*, 1916, and *The Evolution of Man*, 1924, p. 69.

the Pleistocene period—near Heidelberg. The jaw is very large and massive, the flat ascending portion is much broader than in modern man; and there is no trace of a projecting chin. While the teeth are typically human, the general form of the jaw is distinctly intermediate between that of man and that of an ape.

*Homo rhodesiensis.*—This "species" of fossil man is based upon fragments of two skeletons, including a nearly complete skull, from the Broken Hill cave deposits in Rhodesia. The skull is of a peculiarly brutal type, with enormous eyebrow ridges like those of a gorilla, and a great development of the lower part of the face or muzzle. A disquieting feature of the skull is the fact that the teeth are badly decayed. Those who, like myself, have had experience of the life of men under primitive conditions will probably find it very difficult to believe that severe dental caries is compatible with continued existence in the stress of a really wild existence, such as that of man during his early evolutionary stages. Consequently, its presence in the Broken Hill skull will suggest the desirability of keeping a quite open mind as to whether the skull in question is to be regarded as a normal one belonging to an extinct type of man, or merely as an abnormal one belonging to modern man.

Palaeontology, as usual, teaches us only facts regarding the skeleton with the inferences that can be directly drawn from these. On such foundations rest most of the graphic picture of Neanderthal man quoted from Elliot Smith. From the general considerations of comparative anatomy we are justified in believing that in early stages of his

evolution ancestral man was decidedly ape-like in appearance. He had a tail in the adult, as he still has in the embryo. He possessed a covering of hair in the adult, as he still has for a time in the embryo. The great—but very variable—reduction of hair in modern man is probably to be associated with his having learned the advantage, and taken to the use, of movable coverings, primitively of animal skins, later of woven fabric, that could be varied to suit weather conditions. As we should expect on this hypothesis the hairy covering has disappeared particularly completely from the back—the region which the primitive savage covers when protecting himself from the inclemency of the weather. Personally, I believe that we are justified in drawing the further conclusion that in all probability man evolved in a cold climate, not in a warm one as is held by many. In agreement with this we find the remains of Neanderthal man still associated with cold climate mammals, such as the woolly mammoth and the woolly rhinoceros.

We seem again justified in believing that primitive man had a black skin, as still seen in the gorilla and chimpanzee, and in the two races of men—Negro and Australian—that are recognized as being on the whole most primitive in their structure.

The function of the black pigment of the skin is to block out the light rays which undoubtedly have a harmful influence on living substance. We are very apt to lose sight of this direct harmful effect of light owing to its secondary beneficial influences being often more familiar. The destructive effect of light upon the living activities of microbes that cause disease ministers

indirectly to the health of man. Again the mental effect of bright sunshine, with its associated ideas, is of great health-giving potency. But the direct effect of light upon living protoplasm is harmful. Even in the case of a green plant, which is entirely dependent upon daylight for its nourishment, the living activity of the protoplasm apart from nourishment—as shown, for example, by the phenomena of cell-multiplication and growth—is distinctly checked during the hours of daylight. In the more complex animals the body is adapted to withstand this harmful influence, and the most conspicuous factor in this adaptation consists in the provision of a light-proof coat of pigment. The study of the minute structure of the eye in various types of animal affords many beautiful examples of the way in which cells, bordering on the light-flooded interior of these organs but not themselves concerned with the perception of light, are shielded by a dense deposit of pigment.

An interesting point not generally recognized is that the adaptation of the animal body against the hurtful effect of light is really fitted to daylight of the normal composition reaching the earth's surface, including those portions of the spectrum whose waves are too small to be perceived by the eye. Consequently, when in civilized existence particular parts of the spectrum are screened off, as, *e.g.*, the ultra-violet rays by window glass or by smoky atmosphere, the adaptive balance is upset and the harmful effects make themselves apparent.

We may take it then that primitive man had a black skin like that of the negro, and that the comparative paleness of the skin in the majority

of existing races of man is correlated with the diminished importance of the pigment coat under diminished exposure to the light, due to the wearing of clothes and to spending a greater and greater amount of time within the shelter of comparatively dark huts and houses. The temporary darkening of the skin or sunburn, which is brought on by exposure to intense sunlight, is to be distinguished from the racial colour, such, for example, as the dark coppery red of the exposed parts of the skin of the Indian which I have alluded to in an earlier chapter.

The visible record of evolution being laid down in symbols consisting of anatomical or structural features, I have naturally devoted the first section of this chapter to the structural evolution of man; but of course the side of evolution of the most intense practical interest is the functional one. It is not the mere structure of the machine but the work that it does that is of the first importance. It is not the mere structure of the right hand that is the practically important thing—for we see that in the dead hand—it is its " cunning ", the degree to which it accomplishes skilled work. It is not the mere structure of the brain that really matters, it is the intellectual power resident in it.

Amongst the functional developments in human evolution those of the intellect are of by far the greatest moment. Probably no biologist who has studied live mammals, who has kept pet animals, and learned to know their ways and read their expressions, who has learned to circumvent big game by playing his wits against theirs, who has gone through the hateful experience of hunting

apes or monkeys, and read in their eyes the human expressions of suspicion, reproach, fear, no such biologist will, I believe, feel himself justified in asserting that the intellectual powers of man are in their nature fundamentally distinct from those of the lower mammals. But the degree of development of these powers in man far transcends anything known in other animals. The power of reasoning about sensory impressions received from the external world attains in him unexampled development. More especially is this the case in regard to visual impressions. We are not justified in asserting that the eye of man is in itself a more perfect organ than the eye of a bird, in fact we should rather be justified in stating the converse to be the case. But where man is supreme is in dealing with the impressions received through the eye when they reach the centres in the brain. The portions of the brain more particularly concerned (cerebral hemispheres) appear in their earliest stages of evolution in the lower vertebrates to have had to do specially with receiving the impressions from the organ of smell. In the South American lungfish (*Lepidosiren*)—the lowest vertebrate which is able to "sniff" after the manner of the higher vertebrates [1]—the cerebral hemispheres reach an enormous size, while in their dorsal portion is a special region in which nerve-cells are crowded together to form a layer which foreshadows what is termed the cortex of the hemisphere in the higher vertebrates. In *Lepidosiren* this patch of cortex is comparatively small, and it has to do purely with the sense of smell. Passing upwards in the scale

[1] Although it is water, not air, that is drawn into the mouth through the nostrils in the case of the lungfish.

of vertebrates we find that the cortex greatly increases in area, its central portion, where the most active expansion takes place, now termed the neopallium, pushing apart as it were the marginal portions of the primitive cortex which persist even in man as little bits of cortex still devoted to the sense of smell.[1] The neopallium meanwhile reaches an enormous size, special parts of it become linked up to the various apparatuses devoted to senses other than smell—hearing, sight, touch, and other obscure types of sensation. It assumes control of the voluntary movements, the muscles that move particular bits of the body having their control localized in special portions. Its various parts become linked to one another by an inconceivably intricate arrangement of nerve fibrils, and similar fibrils link it up with other parts of the brain. The neopallium thus becomes the great central exchange for messages to and from all the various parts of the body. If we voluntarily move a finger or toe we do so by the activity of the appropriate part of the neopallium. If we feel pain in the finger or toe the sensation is not really in the finger or toe, but in the neopallium; it is set up by the messages arriving there from the injured spot, and is referred to the latter through experience, much as a telephonist refers a voice to its owner according to the wire along which the message comes. There is no reason to doubt that the obscure mental processes involved with incoming and outgoing messages—such as experience or memory, judgment, volition—are also carried out within the neopallium.

There is, I believe, strong reason for accepting

[1] Pyriform lobe and hippocampus.

the view, elaborated especially by Elliot Smith, that an overwhelmingly important rôle has been played in the mental evolution of man by the special development of the sense of sight. This was ministered to first by the primitive arboreal habit; in the lower Primates parts of the cerebral hemisphere specially devoted to this sense are found to be enormously developed. And the erect posture of the body in man himself may be regarded as being primarily compensatory to the narrowing of his all-round view due to descent from the trees to the ground. Personally I take the view that the first important steps in establishing the predominance of the sense of sight were probably related to a more or less nocturnal habit. The primitive significance of the two eyes looking in the same direction as in an owl, a Tarsius, or a man, is, in my opinion, undoubtedly that thereby a more powerful impression is produced in the portion of the brain allocated to receive such visual impressions.[1] This arrangement of the eyes therefore is distinctly advantageous to animals that move about at dusk or during the night. Once in existence, however, it opens the way to the development of stereoscopic vision—so essential for judging distance, and consequently of the greatest importance to a creature leading an arboreal existence, and having to leap from branch to branch. The perfection of stereoscopic vision involves intricate developments in the parts of the brain controlling the muscular arrangements of the eyes, to ensure that the two eyes can be converged accurately on

[1] I am aware that physiologists do not all admit this, but I am convinced by many experiments that such a summation of the impressions from the two eyes does take place.

one point, and focused upon one point, even though that point be away to the side and therefore at unequal distances from the two eyes. The accurate control of the eye movements further renders possible the concentration of the evolutionary increase in the sensitiveness of the retina in the region where it will be most useful.

The steps that have been indicated in the elaboration of the visual apparatus would naturally bring others in their train. While rendering the sense of sight far more efficient for the observation of detail, they would at the same time facilitate conclusions as to the relations of bodies, or parts of bodies, to one another in space. The focusing the two eyes on one point would obviously stimulate curiosity and encourage concentrated attention and closer study of the object observed. The better appreciation of relative position in space would tend to develop greater skill in movement, and the hand being already in existence in the arboreal creature the way would be opened for the beginnings of handicraft.

The right-handedness of man is to be regarded mainly as an expression of the fact that higher skill is obtainable by concentrating education upon one hand than by sharing it equally between the two hands. Ambidexterity is no doubt of use in particular circumstances or in particular professions, but, upon the whole, it is more advantageous to have one hand educated to the higher level attainable by concentrated education. The lopsided development of the forelimbs and their nervous mechanism involved in right-handedness was rendered feasible, in the first instance, by their ceasing to be used as legs for locomotion. The fact that there is a general

tendency to right-handedness rather than to left-handedness raises a very interesting question, and its probable answer is a very curious one. The portions of the brain specially concerned with the faculty of speech are located in the cerebral hemisphere, *i.e.* in a part of the brain which is paired—each hemisphere and each bit of hemisphere existing in duplicate on the right and left sides. But it would appear that the delicate and complex activities involved in the highly skilled faculty of articulate speech have to be concentrated in a single one of the two hemispheres, in order to avoid confusion due to the interference of one with the other. Accordingly, we find this is actually the case, and in the great majority of human beings it is the left hemisphere which has to do with the function of speech. We may take it that this means increased blood-supply and nutrition, and a general increase in functional activity in that hemisphere. But it happens that the muscles of the body by which its movements are carried out are worked by the brain hemisphere of the opposite side—the left hemisphere controlling the movements of the right side and the right hemisphere controlling those of the left side. The right hand has therefore in the normal human being a slight advantage over the left, inasmuch as it is in connexion with the left hemisphere, and we may probably take it that this slight advantage has been the determining factor in deciding that the right hand rather than the left shall reach the higher phase of development. It is of interest to note that in left-handed persons we find, as we should expect, that the speech mechanism is located in the right cerebral hemisphere instead of the left.

It will of course be seen that the various develop-

ments that have been indicated in relation to the sense of sight and its uses would carry with them parallel improvements in these still more obscure operations that we call mental. Colour, form, spatial relations and the muscular movements related to them—whether of the body as a whole in moving from one place of environment to another, or of small parts of the body, as in handicraft; it is only necessary to bring these into relation with experience and memory and judgement, to realize what an enormously important part they have played in providing the mental equipment of man.

Probably the most important of all steps in the higher stages of the mental evolution of man was the development of the use of symbols to represent ideas, so that an idea, or a chain of ideas, could be passed on from one individual to another. Such no doubt originated in mere expression of emotions or feelings; even in the lower animals we find such symbols in common use. The particular type of symbol which became all important in man was that type which is perceived by the sense of hearing. Already in many of the lower air-breathing animals such symbols are in use—of simple character and small variety. Any one who keeps a dog or cat learns to distinguish a number of different inflections of the voice whereby it expresses different feelings; such, for example, as the short sharp bark of a dog that wants a door to be opened, or the cry of a cat in similar circumstances, and the soft sound of acknowledgement when its request has been complied with. In man, however, the use of these sound symbols undergoes an enormous development in correlation with parallel evolution of the organs of voice and hearing, and the part

they must have played in man's mental evolution is apparent as soon as we reflect that language renders possible for the first time the communication in detail of individual experiences to others and, as is particularly important, the discussion of these experiences with others. Through the use of language came one of the greatest steps in man's mental development as compared with that of the lower vertebrates, namely, his comparative emancipation from the dominance of these inherited mental reflexes we call instinct, and the substitution therefor of actions in response to reasoning based upon individual experiences. But it must not be supposed that the rôle played by language in mental evolution is limited to the communication of ideas to, and their reception from, other individuals. It plays a further part of inestimable importance in the whole process of thought—for our thinking is done to a very great extent in word symbols, even when these are not uttered aloud.

While the development of spoken language undoubtedly played a rôle of the utmost importance in the earlier phases of man's mental evolution, its power became enormously increased when the new advance was made of replacing the sound symbols by symbols perceptible to the eye, and thus opening the way to the development of script and printing. Printing for the first time made really practicable the co-operative thinking of mankind; it also made it possible for the individual man to attain in the minimum time the level reached by his predecessors, and so to make a start afresh practically from the point at which they left off.

This use of visible symbols for the communication of ideas has developed independently along two main lines. The first of these had to do with the representation of definite concrete objects by the symbols. The primitive savage had of course no conception of such representation. The first pictures which I showed to the Natokoi Indians conveyed nothing to their minds. A photograph of a man, or a good engraving of a familiar animal, appeared to them as a meaningless smudge. They very rapidly, however, learned to interpret the at first apparently meaningless designs, and to identify a jaguar, or a parrot, or a toucan, or other object familiar in their daily life. The climax came when one day, as the Indians sat round me, one of the chiefs said that he himself would make a picture. I handed him a sheet of paper and a pen, and told him to make a picture of one of his men Chigeranataloi. He laboriously did so, and the result is seen in Fig. 45. This picture is of great interest as being in all probability the very first picture of the human form made by a particular race of primitive men. Like a young child's drawing it in all probability repeats pretty closely the kind of pictures first made by ancient man. Such beginnings of pictorial art evolved in due

FIG. 45.—Portrait of man drawn by a Natokoi Indian.

course in two different directions. One direction led to the higher and higher development of the individual picture, and it is of great interest to note that already in Pleistocene times such pictorial art had reached a very high development, as shown by the marvellous rock paintings and engravings of bison, deer, and other animals that have been discovered on the walls of caves in France and Spain. In the other direction evolution favoured the rapid production of simple more or less conventional representations of objects, so that by stringing these together an extended record could be made. Along this line has developed various written or inscribed or printed languages, such as that of the Chinese—handicapped, however, in usefulness by the great number of the characters required—each in its original form being a simple picture of a particular object.

The other main line along which the communication of ideas through visible symbols has developed is of a much more practical kind, owing to the comparatively small number of its necessary characters. These have come to represent in this case not objects but the ordinary sounds used in speech, and as a consequence language can be expressed in them with a fluency and facility comparable with that of the spoken tongue. It is of course along this line that there have taken place those developments of printing which have played the main part in the evolutionary advance of present-day civilization.

We may then safely admit the dominant part played by the sense of sight in the evolution of man. It has rendered possible the use of the hand for the performance of those delicate and finely co-ordinated movements upon which rest handi-

work and all its developments in art and industry. It has facilitated the development of the imitative faculty in which lie the foundations of education. And, in general, it has been of all the senses the most important in enabling primitive man to live by his wits and press onwards along the evolutionary path.

## The Communal Evolution of Man

One of the most interesting chapters in human evolution is that dealing with the communal evolution of civilized man. That phase of human evolution is governed by precisely the same set of fundamental principles as we have seen to hold in the evolution of other types of community. Primitively, as can still be seen to-day in a few remote regions of the world's surface, the human community is small, composed of but a few individuals. These live entirely by hunting and fishing. They eat such wild fruits as they come across, but they do not plant or sow, nor do they keep domesticated animals. There are natural differences in talent between members of the community: one is more skilled at honey collecting, another at reading trails and tracking wild beasts, but apart from this there is practically no specialization. Each man of the community fashions his own bow and arrow and club; each woman prepares and softens skins for use as garments, or, in a slightly higher stage, weaves garments for her man and, later still, for herself in place of the softened skin. The members of these small communities have no permanent settlements. They are pure nomads, remaining in one spot only for short periods when the conditions for hunting and

fishing are there favourable. Constantly liable to attack by other wandering bands, the little community at once dissolves into its individuals in time of danger.

When comparing such a primitive human community with the civilized community, we see advances similar to those we have seen in animal communities. The highly evolved human community is relatively enormous in size, consisting of thousands or millions of individuals. These are highly specialized into different professions and trades for the carrying out of the manifold activities incidental to the large complex community, and finally the individuals are firmly knitted together by a complicated social organization.

The attainment of the high degree of social evolution that we see in the civilized community has obvious advantages. It brings in its train greatly increased power, and with this power comes increased wealth and increased comfort to all members of the community. One of the lessons taught by life amongst savages in the primitive hunting phase of evolution is, by the way, that even the poorest member of the civilized community leads a life of vastly increased comfort as compared with the primitive savage. He has a roof to shelter him from the weather, garments to protect him from the cold. Supplies of food and water are at hand to save him from the risks of starvation in a bad season when hunting and fishing fail. Transport and amusement are provided, and even if penniless he has at hand the interest and the compassion of the community. Far different is his existence from that of the primitive savage—resting at night uneasily on the bare ground,

exposed to cold and wet, compelled to start off before dawn in the endeavour to get by hunting his bare subsistence, without refuge or surgical help in the event of accidental injury.

But a heavy price is exacted for the advantages of civilization. In the savage community in the primitive hunting stage the level of bodily and mental efficiency is kept up by pitiless elimination, in the never-ending struggle for existence, of individuals lacking in either physical or mental strength. Disease is a rare phenomenon under these conditions, where a handicap no more serious than a sprained ankle may mean death. Enfeebled powers of observation by the senses, or enfeebled powers of reasoning upon observation alike entail serious risk of death from starvation or by attack from human or other enemies. By such selective processes the human community, while still in the primitive nomad condition, is pitilessly kept up to what was called by the recruiting authorities in the Great War an A1 standard.

In the civilized community this heartless keeping up to the high-water mark of efficiency comes to an end. The weeding out of tendency to disease becomes far less ruthless; in fact the dictates of our humanity force upon us rather the saving of individuals with such tendencies, and even the permitting them to contaminate the race by handing them on to the next generation. While the enfeebled are thus protected and encouraged, there also takes place a continuous elimination of the more fit by the fatalities of sport and war, to which they more willingly submit themselves, and by emigration to other countries where they believe that their activities will have freer scope. There

is for the biologist no escape from the conclusion that in the price paid for high civilization is included the inevitable degeneration of the race.

The question is often asked: Does man advance in brain-power with his advance in civilization? Has European man so advanced since, say, the days of the ancient Greeks? It is impossible to give an answer to this question based on direct observation. It is no answer to point to the far greater intellectual achievements of modern times, for these are made under conditions in no way comparable with those under which the ancient thinkers worked. The intellectual worker of to-day starts from an incomparably higher level, based on the vast body of knowledge accumulated in literature, and in addition he has at his disposal all the resources of highly evolved technical methods. If, however, we bear in mind the considerations mentioned in the preceding paragraphs, there would seem to be little room for doubt that intellectual power is to-day not greater but actually less than in the days of the ancient Greeks. This would appear to be an unavoidable consequence of the diminished selection value of intellectual power to civilized man, as compared with the savage whose continued existence is actually dependent on his wits. An additional factor bearing on the matter is that in highly civilized society the more intellectual strains are subjected to the constant handicap involved in selfish limitations of reproduction. All such limitation is to be deplored, for the human individuals with their inherent potentialities constitute the biological capital of the community. Each new crop of infants is an accession to the communal capital. In any one crop may be

included individuals with the potentiality of doing incalculable good, not merely to the community, but to the world—a possible Shakespeare or Newton, a Darwin or Lister—and the prevention of such a one from fulfilling his natural destiny is a crime against the community and the race.

It is accordingly, from the point of view of biology, deeply to be regretted that the academic economist should at times actually advocate such limitation. It already exists to a deplorable extent: it always will exist, but it ought to be honestly admitted that the motive power behind it is simply the individual's regard for himself and his immediate family, his desire for more ample means to render attainable a higher standard of living or, it may be, the entirely excusable desire to make available for his own folk a higher degree of education and culture.

It is always an attractive argument that diminution of the number of individuals will mean a larger share of the world's goods to each. What is consistently ignored is the price payable in the future for such momentary increase in comfort. That price includes a disastrous drop in the earnings of the community, due to the diminution of the number of producers, to the less strenuous production on the part of each under slackened competition, and to the loss of business through under-selling on the part of other countries whose workers are content to go on working hard for a more meagre remuneration.

If it be the case, as seems to be the case in the present phase of human evolution, that social advance necessarily brings degeneration in its train, what is to be the future of human culture? As

already indicated, that future will be to a great extent safeguarded, in a way that it was not in early periods of human history, by the fact that modern culture is embodied in books. Although nations and races will in the future as in the past sink or disappear completely, their culture will be taken over by others in a kind of relay race in which human culture will be passed on from one section of mankind to another.

I have said in the present phase of human evolution, for as regards man's future the working of certain all-important factors cannot be foretold. It may be that his existence upon the earth is doomed to reach an abrupt end. Such has been the fate of the overwhelming majority of those forms of life that have flourished and had their day in earlier periods of the world's history. It may well be the fate of man also, and if this happens apart from the destruction of all life through cataclysmic changes in the physical conditions of the earth's surface, it will probably come about through conflict not with highly evolved forms of life comparable with himself, but rather with lowly organized microbes armed with deadly powers of multiplication, and immune to, or able to break successfully through, the protective arrangements of his body.

It may be, on the other hand, that mankind is fated to go on existing far into the remote future. In this event the races of men that multiply actively will gradually take the place of those that do not, and if they continue to multiply rapidly will lead to such overcrowding of the habitable parts of the earth's surface as will necessarily throw man back under the rigid control of the struggle for existence.

## Evolution and the Race

Evolution being the great principle that is involved in working out the destinies of our kind, it becomes a question of absorbing interest,—To what extent and in what manner can we control and modify the evolution of man? This applies particularly to our communal evolution. We belong each one of us to a particular race of mankind, to a particular nation. We may call ourselves citizens of the world, we may profess the creed of internationalism, we may be honestly fond of some other race among whom we have lived and worked, but if we are normal, sane, healthy, human beings, our strongest ties of affection and interest are with those of our own race and country. The practical question then is: To what extent can we help its evolutionary progress?

There are those, of course, who have no desire for evolutionary progress, who believe in the simple life of the savage, and hold that it would be far better for us to go back to that simple life. Those who have had personal experience of such a life will have much sympathy with the idea. To a young man in perfect health and hard condition such a life has a wonderful charm. For the sake of the liberty and freedom, for the sake of living with Nature and getting to know her ways to an extent impossible in civilization, he is willing to pay the price. But the price is a big one. The clothes the citizen wears, the warm and light yet weatherproof house in which he dwells, the varied foods and beverages brought from the ends of the earth, the transport that carries him hundreds of miles in a day, books and pictures and theatres and concerts,

in fact the total of what to most people makes life worth living, are fruits of our highly complex, highly specialized, civilized society. They are the outcome of human selfishness, the product of men who have been moved to labour with their minds or bodies by the need or desire for money. All these luxuries are included in the price to be paid for a return to a primitive state of society. Those who have actually lived in such a primitive condition, while admitting its charms, will realize that a general return to it on the part of communities weakened by hundreds of years of civilization would, in an inclement climate or in fact anywhere except in a few specially favoured spots on the earth's surface, mean simply speedy extinction.

We may safely take it that the normal members of the highly civilized races have not the slightest desire to throw away their heritage of civilization, but that their aim is rather to keep pressing onwards along the evolutionary path in the honest belief that advance, even though it necessarily entails specialization of individuals and their unequal remuneration, means, on the whole, increased prosperity and happiness to every section of the community.

The chief school of thinkers who believe in the possibility of actually modifying the course of human evolution are the Eugenists, and the method by which they hope to effect this is birth control and regulation. Theoretically there is little room for division of opinion on this subject. It would clearly be to the advantage of the race if the provision of future generations could be left to those possessing the highest types of personality—physical, mental, and moral—and if those who are afflicted

with heritable traits of body or mind or morals that are undesirable could be restrained from handing these traits on to future generations.

The formidable difficulties in the way of effecting anything considerable in actual practice in this direction are mainly emotional and sentimental. Such persons as are willing and able to control their emotions at the behest of reason are precisely the persons whose full representation in the next generation is of particular importance to the community. The lower type, on the other hand, which it would be of advantage to the community to stamp out, is deaf to any such appeal. If, on the other hand, compulsory methods are favoured, as in those American states which have adopted legislation for the compulsory sterilization of criminals, experience has shown that the dictates of our humanity prevent these methods from being carried into practice.

On the whole the indications are that more is to be gained by accepting the natural principles that govern our communal evolution and making the best of them, than by flying in face of these principles. More is to be hoped for as regards the evolutionary progress of man in relation to his community than as regards his evolution as an individual. Accepting the selfishness of the average individual as a regrettable but incontrovertible fact—an unavoidable result indeed of the struggle through the course of ages which has placed civilized man where he is—and recognizing that the entire abolition of this selfishness is not merely an unattainable ideal, but that its attainment would in practice be actually harmful to the community in removing the chief incentive to industry, we

should concentrate our attention upon the regulation and control of that selfishness, so that its workings may be on the whole to the advantage of the community. We should endeavour to attract the capitalist, and encourage him to settle in our midst, not because we consider the acquisition of capital a trait admirable in itself, but for the practical reason that the local utilization of capital, even when the motive behind it is that of anticipated profit to the owner, necessarily involves the distribution of money amongst the local working population. We should realize that it is not to our communal advantage to kill the goose that lays the golden eggs by inspiring the capitalist with the belief that his capital will be more welcome, and therefore more profitable to himself, if transported to some other country, and there used for the employment of foreigners instead of our own kith and kin.

A conclusion that seems quite clear is that the modern democratic community has now reached a condition which threatens its continued evolution with serious danger, owing to the fact that while the community itself has pressed onwards in its evolutionary progress, the training of its citizens to understand and play their part in that progress has not kept pace with this communal advance. The result is that large sections of the community, knowing nothing of the biological and economic foundations of society, untrained in thinking for themselves, are completely without that immunity against the poison of the anti-social teacher that even an elementary education along proper lines would provide. The planning of such a system of education will be a task worthy of the finest avail-

able intellects. Its need is indeed pressing if our communal evolution is to continue along the lines of democracy.[1]

[1] See the present writer's addresses to the Royal Philosophical Society of Glasgow (*Proc. Roy. Phil. Soc. Glasgow*, vols. l., lii., and liv.).

## BOOKS FOR FURTHER STUDY

BOULE. *Fossil Men—Elements of Human Palaeontology.*
SMITH, ELLIOT. *The Evolution of Man.*

# CHAPTER XV

## CONCLUSION; SOME OF THE GENERAL PROBLEMS OF EVOLUTION; SUMMARY

In the preceding chapters of this book I have sketched, in bare outline and so far as possible in simple and non-technical language, the Evolution Theory as it presents itself to me to-day. In deciding what to include in this outline sketch out of the vast mass of current ideas on the subject, I have tried to ignore the passing fashion of the moment, and to be influenced only by a single consideration, namely, the balance of probability, in view of the facts so far as we at present know them, as to what may be counted upon to persist as essential components of the permanent edifice of evolutionary theory.

We have seen that the main fact of the evolution of the animal kingdom is definitely established. Embryology shows the process taking place in the life of the individual, and we have no available explanation of this fact other than that it is a repetition of racial or secular evolution in the past. Palaeontology has revealed to us many little paragraphs in the later pages of the record of this evolution. Comparative anatomy and zoogeography provide innumerable facts that, pieced together, tell the same tale of evolution.

Were our knowledge of the course of evolution complete we should be able to construct a genealogical tree, rooted in the first primaeval living substance, and branching out into all those innumerable branches and twigs, the ultimate tips of which are the various individual living creatures of the present and the past. It need not be said that such complete knowledge is not, and never can be, ours.

As regards the initial and most important step—that whereby non-living substance became living—our ignorance is complete. We may take it as perhaps probable that comparatively large masses of matter were concerned in the progress through increasing complexity that was eventually to lead to life, and that the first pieces that actually lived were able to add to themselves, to grow, by a comparatively simple process of assimilating material in contact with them which was already *nearly* alive.

As regards the earliest stages in which living substance was delimited so as to constitute a definite individual, sharply marked off from its surroundings, we are again in complete ignorance. When, however, we take a general view of animal evolution, we see that one of its striking general characteristics is that it involves on the whole increase in size, until the way becomes barred by limiting physiological conditions. On the whole, large animals are highly evolved and of complex organization; small animals are less highly evolved and of less complex organization. No absolutely rigid law to this effect holds, for there are many exceptions, but there is certainly a general tendency of the kind: an adult vertebrate, or mollusc, or

echinoderm, or arthropod, is normally very much greater in bulk than a protozoon.

We can in a manner understand why increase in size and complexity of structure on the whole go together, for perhaps the greatest characteristic of living things is the constant inflow and outflow of matter and energy at their surface, between the living substance within and the non-living world without. This interchange takes place through the surface, but, as increase in size necessarily brings with it a proportional diminution in area of surface in comparison with the quantity of living substance, it follows that the difficulties in the way of this interchange, or, in other words, the difficulties in the way of remaining alive, become greater and greater as bulk increases.

We are probably justified, then, on these purely logical grounds in believing that the earliest definite living individuals were creatures in the form of exceedingly minute microscopic particles in which the proportion of surface to bulk was very large.

## Filter Passers

During recent years the very important discovery has been made by bacteriologists that there actually exist microbes—particles of living matter—so small as to pass through the pores of fine porcelain filters. They are hence given the name of filter passers. They measure from about $\cdot 5\ \mu$ in diameter downwards—the lower limit of size being quite unknown. Such microbes are believed to be responsible for many human diseases, such as small-pox, scarlatina, hydrophobia, influenza, common "cold". Only the larger types

of such filter passers have been recognized microscopically: it is possible that many are indeed below the limits of microscopic vision.

The filter passers proved to exist are all parasites, but we know that parasitic creatures have been evolved from free-living, and we may therefore, I think, take it as exceedingly probable that there exist myriads of free-living filter passers. I firmly believe, indeed, that the search for and investigation of these constitutes one of the most important tasks immediately confronting present-day biology. In it will probably be found the solution of problems of the greatest importance in relation to the ultimate nutrition of marine organisms, on a knowledge of which so much of practical importance in relation to fisheries depends. From the evolutionary point of view their importance would rest on their recognition as persisting members of the most ancient type of individual organisms, dating from a period far anterior to that in which began to diverge the two evolutionary branches which are now represented by the animal and vegetable kingdoms.

If we accept the probability that the first living individuals were minute creatures of the filter-passer type, the next puzzle which confronts us is the question how did they evolve into the cellular type of organism represented by the whole of the existing animal kingdom from *Amoeba* and its allies onwards? Does or does not a typical cell with nucleus and cytoplasm, such as an Amoeba, correspond to a single one of these primitive organisms enormously enlarged? Upon the whole I am at present rather inclined towards the view that it is

the nucleus alone that we have to look on as the equivalent of the primitive organism, and that the cytoplasm is to be interpreted rather as living substance of a lower grade which the nucleus has elaborated around itself and which it controls. The substance of the cytoplasm would be regarded from this standpoint as living substance, so to speak, on the way towards, but not actually at, the higher grade represented by nuclear substances.

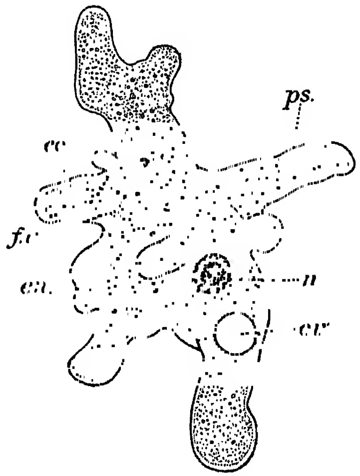



FIG. 46.—*Amoeba*—greatly magnified. (From Graham Kerr, *Zoology for Medical Students*.) *c.v.*, contractile vacuole; *ec.*, outer layer (ectoplasm); *en.*, inner mass (endoplasm); *f.v.*, food-vacuole containing food-particle undergoing digestion within it; *n*, nucleus; *ps.*, pseudopodium—a projecting lobe of protoplasm.

## Evolutionary History of Animal Types

The darkness which enshrouds the origin of the cellular phase of evolution becomes less marked when we turn to the origin of the great divisions or phyla of the animal kingdom as it exists to-day. We find ourselves in a dusky twilight through which we can perceive at least distinct probabilities in the way of evolutionary descent. The frequency of the gastrula stage (Fig. 2, p. 14) in the development of many different types of animals would appear to indicate clearly that the usual portal of emergence from the protozoan phase was by way of one wall of a community of coherent

cells becoming tucked inwards to line a cavity in which the operation of digesting the food was carried on. Such gave rise to the tubular type of creature, closed at one end and open at the other, its wall composed of two layers of cells, which still persists as an adult creature in the world to-day—the little *Hydra* of fresh-water pools and its various relations.

Again there are certain obscure facts of embryology which lead some of those who study such questions to believe that four of the most important phyla of the animal kingdom—the Annelida, the Arthropoda, the Mollusca, and the Vertebrata—emerged from the Coelenterate phylum to which *Hydra* belongs by way of a type somewhat like the existing sea-anemones (*Actinia*, etc.), the long slit-like or dumb-bell shaped opening of this type becoming obliterated, except as regards its end portions which persisted as the mouth and anus of more highly evolved stages.[1]

As regards these main phyla of the animal kingdom, then, we find ourselves justified in forming a definite opinion as to their evolutionary origin. At the same time we should guard ourselves from thinking of any of the more highly developed phyla as we now know them—Mollusca, Arthropoda, or Vertebrata—as being actually ancestral to the others. To hold such a view would involve the assumption that the supposedly ancestral phylum had come down unchanged since the days when the supposedly daughter phylum sprang from it, and the obvious improbability of this could only be countered by weighty evidence such as has not in fact been forthcoming.

[1] Graham Kerr, *Embryology*, p. 493.

It will be realized, then, that we are not in a position to construct a genealogical tree of the animal kingdom with any justifiable pretensions to accuracy of detail. Such trees when made, as they often are, are to be regarded merely as simple and graphic expressions of the views, for the time being, of their author.

While the precise genealogical relations of the main phyla of the animal kingdom to one another remain still, to a great extent, obscure, we have made greater progress as regards the subsidiary sections of these phyla. To take, for example, the phylum to which we ourselves belong—the Vertebrata—I believe that what we now know of the embryology of the more archaic vertebrates [1] definitely justifies us in visualizing the ancestral vertebrate as a creature of elongated worm-like form, provided with numerous feathery gills projecting in a row along each side of its body. We are, in my opinion, further justified in believing that two pairs of those external gills became stiff and rigid, and evolved into limbs by which the owner clambered through the swampy vegetation amongst which it lived. In due course some of these ancient swamp-dwellers adventuring into the deeper waters became highly specialized swimmers, their limbs becoming flattened fins, and so gave rise to the shark-like fishes. At a later period, after a new organ—the lung—had made its appearance, a second emigration into the deeper waters took place, giving rise to the ganoid fishes, and eventually to the teleosts or modern fishes. Another set of emigrants from the swamps

[1] Palaeontology can, of course, offer no useful opinion regarding evolutionary stages earlier than the comparatively advanced ones in which a hard petrifiable skeleton had already come into existence.

took to the dry land. Their limbs, flattening out at the tips and becoming subdivided into digits, and taking on a characteristic double flexure (cf. Fig. 47), became the typical legs of the terrestrial vertebrate. Some of these emigrants, not succeeding in entirely emancipating themselves from the ancestral aquatic environment, still required water as the surrounding medium for the early fish-like stages of their life-history, and even when adult were unable to survive except in a comparatively moist atmosphere. This phase in the evolution of land animals is represented by the group Amphibia (newts, frogs, etc.) of to-day. Another section of

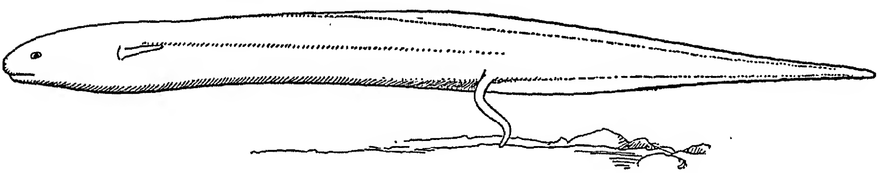


FIG. 47.—Young Lepidosiren, showing the double flexure of the hind limb represented in terrestrial vertebrates by the knee and ankle joints.

these emigrants became more thoroughly specialized for an existence on dry land, their eggs being enclosed in a hard protective shell and provided with a large supply of stored-up food-material in the form of yolk. The young animal, with its ample supply of food, was thus enabled to pass through, in the seclusion of the egg-shell, those fish-like stages which in the case of the Amphibia had still to be passed in the water. These creatures were the ancestors of two diverging groups, the reptiles and the mammals. Of these the first were, above all, characterized by the surface layer of the skin developing a horny impermeable character effectually preventing evaporation from the surface. Of this reptile stock some retained the

primitive lizard-like form, but others diverged in different directions. The Chelonians (tortoises and turtles) assumed a squat type of body enclosed in a rigid case of bone. Some of the lizards developed an elongated worm-like form, accompanied by the reduction and eventual disappearance of the limbs, as in the slow-worm or blindworm and the Amphisbaenids of to-day. The snakes and serpents represent a similar line of evolution carried to a still higher degree of specialization. Still other types of reptiles became specialized for flight. Such were the pterodactyls of Jurassic times; and such, evolved to the highest pitch of perfection, are the birds of to-day, with their splendidly developed powers of flight, the high temperature of their body caused by the great activity of its living processes, and the conversion of the scales into fluffy feathers which, with the air entangled amongst them, serve to retain the heat of the body. The structure of the bird's body shows it beyond question to be a modified reptile. The Jurassic bird *Archaeopteryx* shows features in its skeleton distinctly intermediate between those of modern birds and reptiles, so that it represents a definite evolutionary link. Both *Archaeopteryx* and other ancient fossil birds possess pointed teeth in their jaws, suggesting a fish diet, and we may, in my opinion, take it as probable that their reptilian ancestors were aquatic fish-eaters. In the development of their wonderful air-sacs I see an apparatus which had for its primary function the rapid return to the surface after diving in pursuit of fish, while the air entangled amongst the oily feathers would assist in the same function in addition to impeding the loss of heat. Flight itself I regard as a further

development of swimming under water, in the manner to which the modern diving birds have reverted.

The mammals represent the other great branch of this purely terrestrial stem. In them the skin has not lost so entirely its primitive soft and glandular character as it has in the reptiles, but it has developed as its special peculiarity the coating of hair. This, with the air intermixed with it, carries out the same heat-retaining function as the feathery coating of birds, but, in addition, serves as a sensory apparatus, each individual hair having a sensory nerve connected with it, and serving as a delicate organ of touch projecting into the external world. The most important item, however, in the equipment of the mammals that adapts them to a terrestrial existence is their high development of viviparity, *i.e.* the retention of the egg within the body of the mother until a great part of the early and helpless stages of development has been safely passed through. The two mammals that have departed least from the ancestral type—the Duck-bill (*Ornithorhynchus*) and the spiny *Echidna* of Australia—still retain the ancestral habit of laying eggs, though these are laid at a comparatively late stage in the development of the embryo, and during the latter part of their sojourn in the uterus exercise a newly developed power of absorbing nourishment from the mother. In correlation with this a smaller amount of reserve nourishment in the form of yolk is present, and the egg as a consequence is comparatively small.

In *Echidna* a further stage in evolution is seen, for the female develops a temporary pocket on the lower side of the body, into which the egg

is passed to complete the period of incubation. Eventually the young animal is hatched and still remains in the pouch, nourishing itself by licking up a new secretion from the skin glands of the interior of the pouch. This new secretion is milk.

An evolutionary stage in advance of *Ornithorhynchus* and *Echidna* is afforded by the numerous mammals grouped together as marsupials—from the circumstance that many of them possess a pouch in which the young are carried. The various present-day survivors of this grade of mammalian evolution are found for the most part in Australia, but a few, including the opossums, inhabit the American continent. In the marsupial the egg remains for a longer period within the uterus. The protective egg-shell, no longer necessary, has disappeared; the embryo is nourished entirely by absorption from the mother; and the reserve store of food in the form of yolk is no longer formed.

A point of special interest is that in some of the marsupials the surface of the egg comes into extremely intimate relations with the lining of the uterus, the two surfaces adhering closely together and being richly provided with blood so as to facilitate the exchange of substances between the circulating blood of the mother on the one hand and of the embryo on the other. From the maternal blood there diffuse into the blood of the embryo supplies of food and of oxygen, while in the opposite direction there pass away from the blood of the embryo the carbon dioxide and other waste substances produced by its living activity. With these facilities at its disposal the young marsupial is able to proceed far on its course of development. When eventually born it is passed into the pouch and

nourishes itself with milk, hanging on by its mouth to a teat, through which the milk is sucked.

The final stage is reached in the ordinary mammals. In these the adherent embryonic and uterine surfaces through which the functions of nutrition and so on are carried out have become much more highly specialized, developing into an organ of great complexity, known as the placenta or afterbirth, by which the physiological relations of the embryo to its mother are carried out in the most efficient way. The special advantage of this is that the young animal is enabled greatly to prolong its sojourn in the uterus. There it lives a parasitic existence, its relations with the inimical outer world conducted entirely through the mother, a fully equipped adult individual. The advantage of being thus freed from the direct struggle for existence during part of these early and comparatively helpless stages of life is obvious. The degree of development reached by the time that birth takes place differs greatly in different mammals, bearing a distinct relation to the degree of exposure to the dangers of the outer world involved in the habits of the particular species of animal.

Still another part of the equipment of the modern mammal should be mentioned, as it has undoubtedly played a most important part in contributing to the success of the Mammalia as an evolutionary group, and that is their high degree of intelligence, associated with a special development of the cerebral hemispheres.

In the course of their evolutionary history the mammals have taken up the most varied modes of life, and show corresponding specialization in their structure. Typical examples of such specialization

are afforded by the horse or the antelope adapted to rapid movement on dry ground, by the monkeys adapted to a climbing arboreal existence, the mole adapted to burrowing, the bat adapted to flight, and the whales and manatis to a swimming existence.

While intense specialization of structure to fit present circumstances and mode of life makes for success in the struggle for existence, that success is liable to be of a temporary kind. For high specialization means diminution of adaptability, and, as a consequence, highly specialized types, debarred from adaptive evolution when circumstances change, are apt to come to an end when these circumstances do change. If, therefore, we endeavour to forecast the future of the Mammalia—or indeed any other of the great groups of the animal kingdom—we should probably be justified in anticipating that the future will lie rather with the less specialized types which, in spite of their lack of specialization, are yet able to hold their own, and which as time goes on may be expected to give rise to more intensely specialized branches to fit the special circumstances of the moment.

## Evolutionary History of Organs

To my mind the most striking achievements of evolutionary science up to the present time are not the fairly certain establishment of bits of pedigrees of different types of animals, but rather the successful working out of the evolutionary history of certain of the organs that constitute the body of the more complex animals. I have quoted in Chapter III. a peculiarly impressive example of

this provided by palaeontology, demonstrating how the peculiar stilt-like leg of the horse, terminating in a hoof instead of in a set of toes, has arisen by a process of gradual evolutionary change from an ordinary type of foot provided with digits.

I will now quote another example culled from the field of comparative anatomy and embryology, the particular example being chosen partly on account of its inherent interest, partly on account of the widespread ignorance regarding modern advances in our knowledge bearing upon it.

One of the highly successful groups of present-day vertebrates is that which includes the ordinary fishes of fresh and sea water (Teleostei). The typical fish shows an exceedingly high degree of adaptation to a free swimming existence independent of a solid substratum. The body is of a stream-line form, and its main organs are concentrated towards the head end, the hinder portion of the body being devoted entirely to propulsion, its end being broadened out in the tail fin, so as to make more efficient the strokes produced by the contraction of the great laterally placed muscles. The two pairs of thin flattened limbs are comparatively small, and are used mainly for balancing. The surface of the body is lubricated by the continuous oozing of exceedingly slippery slime from thousands of minute glands scattered throughout the skin.

Included in the equipment of the fish is an organ called the air-bladder or swim-bladder. This is typically an elongated closed cavity lying immediately underneath the backbone and filled with "air". The main function of this air-bladder is a hydrostatic one; it serves as a float, to keep the

body of the fish at precisely the same specific gravity as that of the water in which it swims, so that it can hang motionless in the water at one level without wasting muscular energy in swimming to counteract the tendency to sink into the depths. It will be seen that this function involves complications. Suppose a fish in the sea is hanging about at a particular depth, say a hundred fathoms, attracted by its favourite food being particularly abundant for the moment at that level, and suppose it now swims downwards to a greater depth. As it swims downwards the pressure of superincumbent water will increase—each thousand fathoms of depth involves a pressure of over one ton per square inch—and this increase of pressure will compress the air in the air-bladder and so, by increasing the specific gravity of the fish, bring about a constantly increasing tendency to sink downwards. On the other hand, if the fish starts to swim upwards from its hundred fathom starting-point, the diminishing pressure will allow the air in the air-bladder to expand, and so, by diminishing the specific gravity, will tend to cause the fish to be carried up helplessly to the surface. It will not suffice, then, for the air-bladder to be a mere float; it must have some compensatory mechanism to counteract the two dangers I have indicated. Such actually exists. In the first place, there are present patches of gland-cells in the lining of the air-bladder which have the power of extracting oxygen from the blood and passing it in gaseous form into the cavity of the air-bladder. Through a complicated nervous mechanism these gland-cells are set to work when the fish is subjected to greater pressure through swimming downwards, and the increase so brought

about in the amount of gas contained in the air-bladder is such as to compensate precisely for its diminution of volume caused by the increase of pressure.

Another part of the air-bladder lining possesses the converse power; its cells, when brought into activity, extract gas from the air-bladder and pass it away in solution into the blood so that it ceases to have any buoyant effect.

In the living fish, through the working of the nervous system, the two processes that have been indicated are nicely adjusted to the varying conditions of pressure, so as to keep the body of the fish exactly at the specific gravity of the surrounding water.

Such is the main function of the air-bladder. There is little doubt, however, that it also carries out a sensory function, making the fish conscious of changes in pressure, and acting, as it were, as a living aneroid barometer. In many fish it is also connected directly with the internal ear, and probably plays a part in making the fish more sensitive to sound or other vibrations in the water.

It is clear, then, that in this air-bladder of the fish we have to do with an organ of great physiological interest. What do we know regarding its evolutionary history? The information we now possess on this subject is provided, as has already been indicated, partly by comparative anatomy and partly by embryology. Embryology tells us that the air-bladder is really an appendage of the alimentary canal, for if we study the development of any ordinary fish we find that the air-bladder makes its first appearance as a little pocket-like outgrowth of the roof of the alimentary canal.

This outgrowth increases greatly in size, and in typical cases loses completely its original connexion with the alimentary canal. Comparative anatomy shows, however, that there are many fish, such, for example, as the salmon or trout or herring, in which even in the adult the primitive opening from the alimentary canal is retained. Comparative anatomy discloses two other facts which we should note, namely (1) that in certain cases the opening from the alimentary canal is not, as it usually is, in the mid-dorsal line, but well down on the right side; and (2) that in a few cases the wall of the air-bladder, or part of it, possesses the detailed structure which is characteristic of a typical *lung*. Observation of such fish when alive shows that they actually use their air-bladder for breathing air, and that if forced to rely entirely on their gills for this function, for example through their access to the surface of the water being prevented by wire-netting, they are drowned in spite of their being fish.

Now when attacking an evolutionary problem like this one of the air-bladder it is wise, after exhausting the evidence to be obtained from the particular group of animals concerned—in this case the modern or Teleostean fishes,—to turn from them to such other groups, if indeed such are known to exist, as the general weight of evidence points to as being more archaic, less advanced along the evolutionary path than the group which is being investigated.

There are actually in existence to-day a number of different fishes which undoubtedly represent ancient types that have advanced less far along the path of piscine evolution than have the modern teleosts. Amongst these are the ganoid fishes, including,

on the one hand, the sturgeons and the gar-pike (*Lepidosteus*) and bowfin (*Amia*) of the great fresh-water lakes of North America, and on the other, *Polypterus* of the rivers of tropical Africa. Another admittedly archaic group of fishes, though farther removed from the evolutionary line that has culminated in the teleosts, is that of the Dipnoi or lung-fish, with one surviving representative in South America—*Lepidosiren*, one in tropical Africa — *Protopterus*, and one in Queensland — *Ceratodus* (Fig. 21, p. 71).

When we refer to the ordinary ganoids we find that they possess an air-bladder like that of the teleost, retaining throughout life its opening from the alimentary canal, and in the majority being used as an additional breathing organ or lung.

One of the ganoids — the bowfin — shows a peculiar feature in the blood supply of the air-bladder, inasmuch as this blood supply is derived, not, as is usual, from the dorsal aorta, the main artery that runs along the body immediately underneath the backbone, but from an artery on each side which corresponds exactly in its relations with the blood-vessel that supplies the lung of the terrestrial vertebrates, and is known as the pulmonary artery.

When we pass down to the most archaic of all the surviving ganoids—*Polypterus* (Fig. 48)—we find there the key to the whole position. If we were to confine our attention to the hinder part of the body, if, for example, we studied transverse sections through the hinder part of the trunk, we should see a perfectly typical-looking air-bladder (Fig. 49, B, *r.l.*), just like that of a teleost or one of the other ganoids. If, however, we trace this air-bladder forwards (Fig. 49, A) we find it no

longer in the middle of the body, but well over towards the right side, while it is now balanced by a corresponding organ on the left side. Tracing

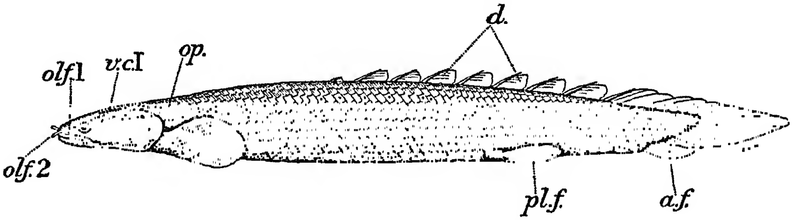



FIG. 48.—*Polypterus*. $\times \frac{1}{3}$. *a.f.*, anal fin; *d.*, dorsal fins; *olf.* 1 and 2, openings of olfactory organ; *op.*, opercular or gill opening; *pl.f.*, pelvic fin; *v.c.*I., spiracle.

the two organs forward, we find that they meet together underneath the alimentary canal, into

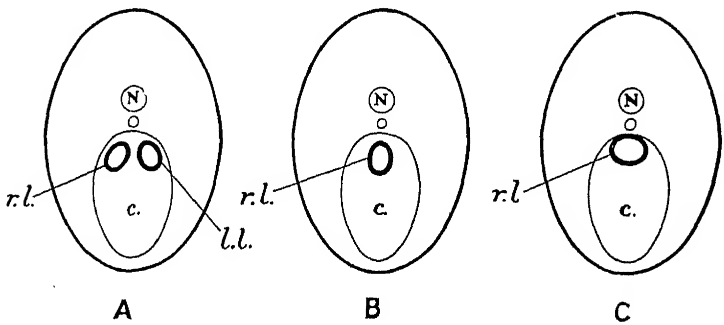



FIG. 49.—Diagrammatic transverse sections through bodies of fish, showing the position of the air-bladder. A, *Polypterus*, section through the front part of the body-cavity, showing the two lungs symmetrically placed. B, *Polypterus*, section through the hinder part of the body-cavity showing the right lung. C, Teleost, section through the body-cavity of a Teleost, showing the right lung or air-bladder. *c*, cavity of body; *l.l.*, left lung; *N*, notochord; *r.l.*, right lung.

which they open by a slit-like opening on the ventral side of the alimentary canal.

If, now, we turn again to embryology, we find that the air-bladder of *Polypterus* is in its early

stages identical with the lung of terrestrial animals; it is a pocket-like outgrowth of the ventral wall or floor of the alimentary canal, which presently divides into two lobes, the right lung and the left lung, communicating with the cavity of the alimentary canal by a ventrally placed slit—the glottis. Further, it comes to be supplied with blood by a typical pulmonary artery on each side, and it has also got a typical pulmonary nerve, just as is the case with the lungs of a terrestrial vertebrate. Finally the organ is physiologically a lung, and the *Polypterus* is drowned if it is unable to reach the surface of the water to fill it with air.

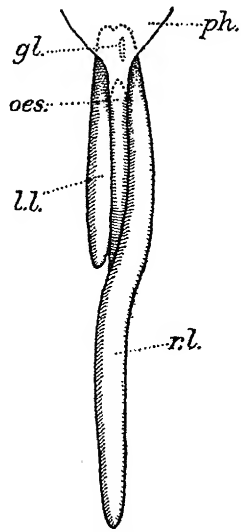



FIG. 50.—View of the lungs of an adult *Polypterus* as seen from the dorsal side. *gl.*, glottis or opening from the pharynx, or anterior portion of the alimentary canal, into the lung; *l.l.*, left lung; *oes.*, oesophagus or gullet; *ph.*, pharynx; *r.l.*, right lung.

*Polypterus*, however, is characterized by the possession of a dense bony skeleton and a coating of dense ganoid scales, and the air-filled lung fulfils an important function in counteracting the weight of these, *i.e.* it takes on, in addition to its primary breathing function, a secondary one as a float.

The two lungs are for a time equal in size, but as development goes on the left lung lags behind in its growth, and it never extends so far back as does the longer right lung (Fig. 50). This lop-sidedness of the lungs would tend to turn the fish over on to its left side, but this is obviated by the hinder part of

the right lung, *i.e.* the portion which is no longer balanced by its fellow on the left side, taking up its position in a median and dorsal position directly under the backbone (Fig. 49, B, *r.l.*). A consequence of this is that the whole arrangement becomes symmetrical, and the overturning effect of the right lung is counteracted.

The bearing of all this upon the evolution of the air-bladder is clear. *Polypterus* has for a time when young a perfectly typical pair of lungs, like those of any terrestrial vertebrate, but a tendency develops for the left lung to be reduced in size as compared with the right, and following upon this the right lung assumes a median position where no longer balanced by the left.

What would happen were this tendency to reduction of the left lung to be allowed continued play until that lung had disappeared entirely? Clearly the *whole* right lung would now have acquired a mid-dorsal position, except its connexion with the ventral glottis, which would take place round the right side of the alimentary canal. Such a stage, intermediate between the ventral pair of lungs and the dorsal air-bladder, is found actually existing in one of the lung-fish, namely, *Ceratodus*.

The air-bladder of the young teleost is precisely the same, except that the unnecessarily long communication between air-bladder and alimentary canal has become shortened up so as to bring the glottis into a mid-dorsal position at the shortest possible distance from the air-bladder.

Thus, then, if we piece together the various facts that I have indicated relating to the comparative anatomy and embryology of the air-bladder, as is done in Fig. 51, we see that they form a paragraph

of evolutionary history which tells us how the air-bladder of the modern fish has evolved out of what was originally the right member of a pair of lungs.

In Chapter II. I have already mentioned other

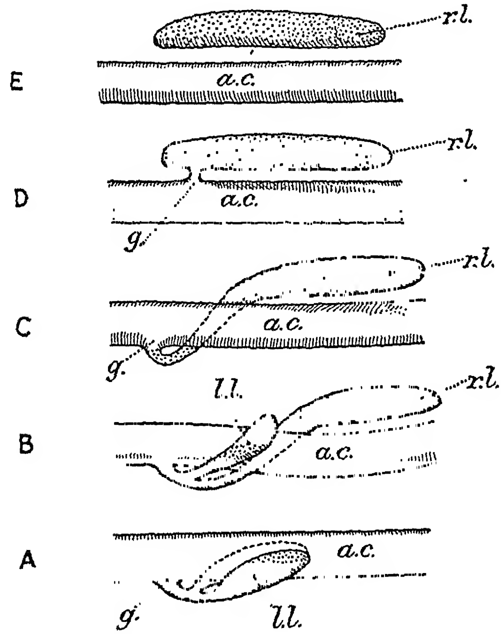



FIG. 51.—Diagram to illustrate the evolution of the air-bladder of fishes. The organs are viewed from the left side. A, primitive arrangement with right and left lungs equal; B, *Polypterus* with left lung relatively reduced; C, *Ceratodus*, the left lung has disappeared entirely; D, one of the more primitive Teleosts in which the glottis has taken up a dorsal position; E, one of the more highly developed Teleosts, in which the primitive connexion between lung and alimentary canal has disappeared. *a.c.*, alimentary canal; *g*, glottis; *l.l.*, left lung; *r.l.*, right lung.

paragraphs of evolutionary history disclosed by embryology, such as, for example, that dealing with the great arteries of the higher vertebrates including man, which are seen to evolve out of an arrangement of hoop-like vessels adapted for the

conveyance of blood to and from the gill openings once, though no longer in the case of the higher vertebrates, used for breathing.

## Some of the General Principles of the Evolution of the Animal Body

Apart from the working out in detail of the evolutionary history of organisms, or organs, immense progress has been made in worrying out general principles concerned in evolutionary change.

A fascinating field for such investigation is that relating to the increase in the size of the individual body, which we have already seen to be a common feature of evolutionary progress, and to the successful tackling of the various physiological difficulties incidental to such increase in size. Such a difficulty of a simple kind is due to the effect of gravity, and we see this met in two different ways, exemplified respectively by microscopic animals and by those of larger size. In very small organisms, such as those of the filter-passer type, the effect of gravity is very small, and the proportion of surface to mass so large that these organisms sink in water with such extreme slowness, retarded by the viscosity of the surrounding medium, that practically they may be said to remain in suspension, the slight convection and other currents that are always present being quite sufficient to counteract the slight tendency to sink. Increase in size, however, does away with this state of affairs, and the creature would naturally sink to the bottom. Many animals have retained, however, the habit of living free in the water. In such cases there frequently are special floats to

diminish the specific gravity—in the case of Protozoa vacuoles, full of watery fluid less dense than sea-water, or of gas or of oil; or in the case of large animals thick deposits of fat under the skin (blubber of whales), or the air-bladder filled with gas secreted by the animal already alluded to in the case of fishes. Among microscopic creatures a favourite

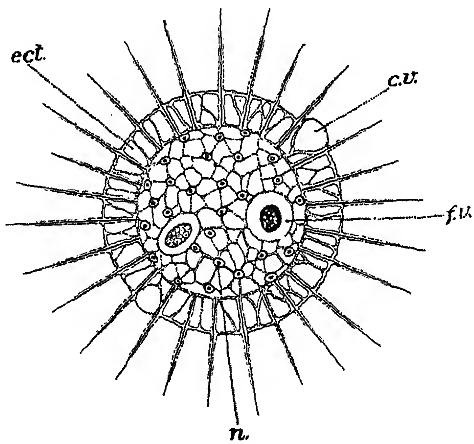



FIG. 52.—A Heliozoon (*Actinosphaerium*), highly magnified. (From Graham Kerr, *Zoology for Medical Students*.) *c.v.*, contractile vacuole; *ect.*, ectoplasm; *f.v.*, food vacuole; *n*, nucleus.

device is simply to continue to make use of the viscosity of the water by a great expansion of the surface of the body through the formation of delicate projections. In some Protozoa we find a temporary floating phase in which this is effected by the cytoplasm projecting into long stiff slender pseudopodia. In still others, such as the Radiolarians and Heliozoa (Fig. 52) and pelagic Foraminifera, this becomes the normal condition. In small crustaceans (Fig. 53) we find quite commonly such permanent extensions of the body to give increase of surface.

In the larger types of animal the chief harmful tendency of gravitation is to distort the shape of the body. Were an amoeba to grow to a thousand times its natural bulk it could no longer retain its characteristic though ever-varying form—its fluid protoplasm would simply become extended out into a thin film—an impossible condition, as most of the cytoplasm would be beyond the control of the nucleus and would therefore die. Accordingly, we find as the animal body increases in size that a system of more or less rigid supports is developed

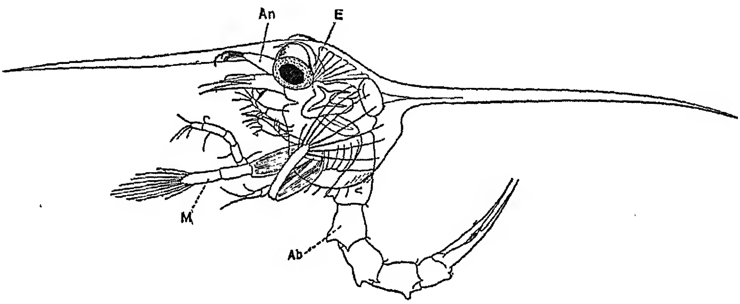



Fig. 53.—Young crab—Zoaea stage. (After Gurney, from *Cambridge Natural History.*) *Ab.*, abdomen ; *An.*, antenna ; *E*, eye ; *M.*, mandible.

to form a supporting framework or skeleton. In one of its simplest forms this may consist merely of cells distended with fluid under pressure. The forerunner of the backbone — the notochord — for example, consists of a rod built up of such distended cells, so that the whole forms a stiff elastic support. More usually, however, solid masses of stiff material are formed by the living activity of the protoplasm. Very different materials are used in this way in different types of animals. They may be simple chemical salts, such as the silica or flint which forms the beautiful skeleton of many radiolarians and

sponges, or the calcium salts, which give rigidity to the bones of vertebrates or the shells of shell-fish. In many cases the skeletal material is waste material produced in the living activity of the creature which, instead of being got rid of as formed, is retained for at least a time and used to support the body. Such is the case with the skeleton in the great group of the Arthropoda, including insects, spiders, and crustaceans. In this case the skeleton is formed on the outside of the body (exoskeleton), such an arrangement having the additional advantage that it serves also to protect the living body like a suit of armour.

Intimately related to the increase in the size of the body is the intense specialization of different members of the cell-community for carrying out the various vital functions already dealt with in Chapter XIII.

In spite of the complex organization of the body expressed in the evolution of the various organs, there comes eventually a limit beyond which increase in size is no longer profitable. The position of this limit differs greatly in different types of animals, according on the one hand to their general plan of construction, and according on the other to their habits. Thus, in the annelid type, such as the earthworm, where the support of the body is given by its distension with fluid, or in the arthropod, where the supporting material is confined to a layer on the surface, the limit is at a much lower level than in the vertebrate, where the body is supported by bony struts traversing its interior. Or, again, flying animals have a lower size limit than running, and running animals lower than those which swim and float—their bodies

buoyed up by the denser aqueous surrounding medium.

But, in any case, increase in size with the increased power that goes with it ceases eventually to be advantageous, owing to the working of many and varied limiting factors, such as bodily weight, food supply, and so on, and then it comes to an end. We should be careful, by the way, to avoid the common popular fallacy of supposing that the creatures of the past which attained to gigantic size, such as the enormous Jurassic and Cretaceous reptiles, became extinct merely as a direct result of their becoming too large and unwieldy. We may rest assured that even the final steps towards that gigantic size were justified by the conditions under which those creatures lived and evolved, and that their eventual disappearance was rather brought about by some change in their environment with which they had not retained sufficient variability successfully to grapple,—it may be some change in purely physical conditions, it may be the appearance of better-equipped competitors, it may be through defeat in the conflict with some unaccustomed type of microbe.

## Evolution in Relation to the Surrounding Medium

Another fascinating chapter of evolutionary philosophy deals with the relations of animals to the medium in which they live.

Protoplasm is a fluid material, and contains normally a large proportion of water. Primitively, in the unicellular phase, the surface of the cell is normally bathed in water as the surrounding

medium. The onward progress of evolution has involved, however, a more and more complete withdrawal from direct contact with the external watery medium. As the body increases in size all the cells of the body, except those on the surface, lose their direct relation to the water outside. There is still, however, a considerable quantity of water enclosed within the external limiting layer of cells, and this watery fluid constitutes an internal medium of the body by which all the internal cells remain bathed.

In the case of an ordinary water pool its animal inhabitants extract from the water the food-material and oxygen necessary to their metabolism, while, on the other hand, they pass back into it the indigestible remains of their food, carbon dioxide, and all the various waste products of their living activities. Thus, if the pool is densely crowded its waters come to be laden with the various substances passed into it by its living inhabitants.

So also with the internal medium of the body. Peopled by its myriads of cell-inhabitants it becomes laden with the products of their living activity. But varied as are their living activities in correlation with their varied functions, so also are their contributions to the internal medium. It follows that the internal medium of the body, instead of being pure water, is a watery solution and suspension of great complexity, but, at the same time, of definitely ordered complexity—each type of cell or tissue or organ contributing its own special quota.

Just as aquatic Protozoa are adapted to live in fresh-water of a particular type, or in sea-water

of definite constitution, so are the cells of the body adapted to live in its internal medium of definite normal composition. Any marked departure from the normal, such as may be caused by one organ or set of cells failing to pay in its normal contribution, is liable to disturb the health of the cell-community. It is a point of great interest, however, that *slight* changes, such as are liable to occur during the normal life of the individual, are made use of to bring about appropriate physiological reactions. Thus, in the more complicated creatures, such as vertebrates, a very slight increase in the amount of carbon dioxide in the internal medium at once produces increased activity in the breathing movements. Or, again, the slight change brought about by the presence of food entering the intestine from the stomach at once induces an increased secretion of the pancreatic juice required for its digestion.

In a comparatively lowly organized creature like a jelly-fish the copious internal medium is practically sea-water, but already it has developed a certain independence of the water outside, for it has been ascertained in the case of jelly-fish liable to find themselves occasionally in fresh-water through floods or rains, that in such circumstances the internal medium departs little from its normal character. Even in the higher animals the internal medium of the body still, as regards its general physical and chemical characteristics, retains a wonderfully close resemblance to the sea-water, the ancestral external medium.

Already in the case of marine animals the shutting off of the internal from the external medium has come about, but this becomes of

greater moment in fresh-water creatures and in terrestrial animals. In the latter the external medium is air, and, consequently, evaporation from the surface of the body brings about a danger of desiccation. In the reptiles, as already mentioned, this is guarded against by the surface of the skin developing a horny layer practically impermeable to water. In the mammals, however, the impermeability of the outer skin is less marked, and the oozing of moisture over its surface is made important use of for cooling the surface by evaporation, and thus helping to regulate the body temperature by antagonizing the heat production associated with the high activity of the vital processes.

### The Arthropods as Terrestrial Animals

It has already been indicated that the earliest types of animal to make their appearance in evolution were undoubtedly inhabitants of the water. Even to-day all the simpler existing types are aquatic. Of the myriads of more complex creatures that have taken to the land and breathe air the great majority belong to two of the main groups or phyla—the Arthropoda and the Vertebrata.

As regards the former of these, the phylum which includes a far greater number of species than any other, such as the Tracheata (beetles, flies, and other insects), the Crustacea (lobsters, shrimps, crabs), and the Arachnida (King crabs, scorpions, spiders, mites)—the present writer differs from his colleagues in regarding them as *primarily* terrestrial. In other words, he believes that all forms of arthropod existing at the present day are descended from a common ancestral type which had taken to a land

existence, and that such arthropods as are to-day aquatic (Crustaceans, and occasional insects and Arachnids) are so because they have reverted to the aquatic habit after a prolonged sojourn during the course of their evolutionary history on land.

Amongst the reasons for taking this view the two chief may be indicated :

(1) It is generally admitted that by far the most primitive of the arthropods known to exist at the present day is *Peripatus* (Fig. 20, B, p. 63) ; it is so primitive in its structure as to form a definite connecting link between, on the one hand, the arthropods, and, on the other, the annelids or segmented worms from which the arthropods, as is generally agreed, have originated in evolution. Now *Peripatus* is purely terrestrial in its habit.

(2) One of the most characteristic and most puzzling peculiarities in the structure of the arthropods seems to find in this way its only reasonable explanation. The peculiarity in question is that in these animals the blood-system has undergone a remarkable modification, inasmuch as the normally tubular blood-vessels have degenerated into an irregular spongy meshwork. When we consider the very active movements of the Arthropoda this puzzle becomes all the greater, for high activity means high consumption of oxygen and great production of carbon dioxide, and this normally involves in turn a high degree of efficiency of the blood-system in correlation with the fact that this serves for the transport to the living tissues of the necessary supplies of oxygen, and for the transport from them of carbon dioxide. Now in the air-breathing arthropods, including *Peripatus*, this respiratory function of the blood-system is other-

wise provided for by a new mechanism in the form of delicate air-tubes or tracheae which, opening at their outer ends to the exterior and dividing into finer and finer branches, serve to convey air directly to all the living tissues of the body. That the appearance of this new system of air-tubes and its taking over one of the main functions of the blood-system should lead to degeneration of the latter is just what would be expected, while without such an explanation this degeneration in the case of actively moving creatures seems incomprehensible.

On these and other grounds, then, I regard the Arthropoda as fundamentally terrestrial, air-breathing animals, and the many types of arthropods that to-day inhabit the waters of the earth I regard as having, in all probability, spread back into the water from the land, and there undergone new sets of evolutionary changes in re-adaptation to an aquatic existence.

As regards the Vertebrata, the other great group which has been successful in colonizing the land, I have already on pp. 247–252 indicated some of the main evolutionary steps associated with this process.

I may appropriately finish this chapter by summarizing in a few words the general position taken up in this book regarding the evolution of the animal kingdom. The main fact that the animal kingdom, as we know it to-day, is the result of a slow process of secular evolution may be taken as demonstrated. The fact of inheritance, and the fact that inheritance, like all other features of living matter, is inconstant and variable—cases

of obviously less complete inheritance being what are commonly spoken of as variations—may also be accepted unquestionably as providing the raw materials for evolutionary progress. Variability, being as I take it simply one of the expressions of that instability which constitutes one of the inherent and most characteristic features of living substance, has to be accepted as a basic fact, and speculation as to its cause is for the present futile. As to the method by which variation is controlled and guided along definite paths so as to bring about evolutionary progress I regard the Darwinian hypothesis of natural selection, with certain modifications in detail, as still holding the field; firstly, as being truly scientific, inasmuch as it does not call in the assistance of factors whose existence is not scientifically demonstrable, and secondly, because the Darwinian principle is actually at work in nature as has to be admitted even by those who would minimize its potency. I adhere to the position of Darwin that the potency of natural selection is in actual fact enormous; I hold that the attempts that have been made to minimize its importance are to a great extent fallacious, invalidated in some cases by their authors' want of experience and skill as field naturalists, and in others by the making of unwarrantable assumptions. Amongst these latter is the absolute "purity of the gametes", as assumed by those who hold that "pure" hereditary substance is wholly devoid of the general property of variability. On the other hand, the natural selection theory has been greatly fortified since Darwin's day by the recognition of Mendelian inheritance—the fact that a particular characteristic is liable to be

transmitted through long series of generations without any obvious reduction or dilution. Further reinforcement is brought by the constant additions to our knowledge of the utility, *i.e.* the adaptive nature, of particular characteristics amongst animals living under natural conditions. Most important aid to the theory has come from advances in our knowledge of physiology, inasmuch as we have now learned how closely dependent the organs of the body are on one another, and how change in a particular organ is liable to bring in its train extraordinary and unexpected changes in other parts of the body. As a consequence, we now recognize how the evolution of a directly adaptive character is liable to bring with it a train of associated unadaptive characters. Thus the natural selection hypothesis, which primarily explains the evolution of adaptive structure, affords indirectly a possible explanation of unadaptive features as well. Another added strength to the Darwinian Theory is the recognition that a particular "variation" is the outward expression of a *tendency* to vary in that particular direction, and that, as a consequence, the selection of variations in a particular direction involves a necessary intensifying of the tendency towards that particular variation, and in turn the encouragement of evolutionary progress along a definite directed line.

# INDEX

THE END

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